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RHIZOCTONIA CROCORUM (PERS.) DC. AND R. SOLANI KÜHN (CORTICIUM VAGUM B. & C.), WITH NOTES ON OTHER SPECIES

B. M. DUGGAR

Physiologist to the Missouri Botanical Garden, in Charge of Graduate Laboratory
Professor of Plant Physiology in the Henry Shaw School of Botany of Washington University

The form genus *Rhizoctonia* was established in 1815 to include two parasitic species, both characterized in part by the production of a mat of violet mycelium investing the affected roots or other submerged members. The serious root diseases due to these organisms (later included in one species) have received consideration by many mycologists since that time. The demonstration is comparatively recent, however, that several important types of root and certain stem and other diseases of a variety of hosts are induced by two or more related species of this genus.

The literature of Rhizoctonia diseases has grown enormously in the past fifteen years, yet some unnecessary confusion and difference of opinion exist regarding the two main species or groups of species and their distribution and relation to disease in plants. This is in part due to the lack of comparative study and to the neglect or inadequacy of herbarium material. It seems well, therefore, to present a conspectus of the investigations relating to this subject, and to include such comparative data as are available.

In coöperation with Mr. F. C. Stewart of the New York (Geneva) Agricultural Experiment Station, I undertook, in 1898, a general study of the relation of *Rhizoctonia* to plant diseases in America. This joint investigation followed two

independent studies, one of a serious root disease of the sugar beet, the other of a destructive stem rot of the carnation. A preliminary report upon the investigations relating to *R. Solani* Kühn was published ('01), and it was arranged that in the further work one of us would undertake the morphological, cultural, and taxonomic aspects of the study, and that the other would assume responsibility for all cross inoculation and field work. Unfortunately for this purpose a change of position on the part of one of us and the demands of other work necessitated the abandonment of the plan as proposed. It is to be regretted particularly that the systematic inoculation experiments which had been carried forward for two seasons could not be continued and published. It is understood, however, that an extensive study in the relations of the culturable forms on different hosts has been carried forward both by cultural and inoculation experiments at the University of Illinois by Dr. George L. Peltier, who has already presented a preliminary report ('15), on the subject. It is mainly a general account of the diseases with notes on comparative morphology that I am able to include, but it is hoped that this may serve to clear up the more obvious difficulties and to suggest some problems requiring special investigation.

The writer wishes to acknowledge the assistance, mentioned in the text, of many mycologists who have furnished material during the progress of these studies, and especially the coöperation of Mr. F. C. Stewart, who contributed many of the American hosts during the earlier studies. To Prof. E. A. Burt I am also indebted for suggestions.

The Violet Root Felt Fungus, Rhizoctonia Crocorum (Pers.) DC.

Early pathological studies

The first mention of a plant disease which may be referred with certainty to *Rhizoctonia* as the causal agent is an important paper by Du Hamel (1728) read before the Paris Academy. In this paper he gives a careful description of a fungous disease of *Crocus sativus* (saffron) occurring in France. His description of general pathological features

leaves little to be desired, and one cannot mistake the fact that he was discussing the disease, later known to be due to *Rhizoctonia Crocorum*. He does not describe the more minute morphological features, but discusses the macroscopic appearance of the mycelium and sclerotial stages with such completeness that no doubt remains concerning the identity of the fungus. The illustration included would likewise confirm the description. He regarded the sclerotium, "tubercule," as the fruit body of a fungus allied to the truffles, and to this special form of body, assumed to bear the organs of reproduction, he gave the name "tuberoides." He likewise determined that a similar fungus is the cause of a disease found upon the roots of *Sambucus Ebulus, Coronilla varia, Ononis spinosa, Muscari* sp., and perhaps other plants.

It was more than fifty years later that Fougeroux de Bondaroy (1785), discussing primarily a disease of the saffron known as "tacon" gives further notes on the "mort du safran," recording the occurrence of this disease on asparagus when following (in the same soil) diseased crocus.

After a further considerable lapse of time De Candolle (1815) made a careful study of the pathology of a similar alfalfa (*Medicago sativa*) disease in the vicinity of Montpellier, but known throughout France. This led to the establishment of the genus *Rhizoctonia* as noted later. It is necessary to the pathological account to note here, however, that he recognized two species, *R. Crocorum* DC., primarily inhabiting the crocus, and *R. Medicaginis* DC., on the alfalfa and other hosts. He did not follow the development of the fungus on the saffron, where host characteristics render somewhat obscure the appearance of the fungus; and so for a long time the continuous violet felt of mycelium was associated primarily with *R. Medicaginis*.

Among other diseases of the carrot and beets in Germany, Kühn ('58) found typical rots of these root crops, accompanied in both cases by a red-violet mycelium with other characteristics indicating the alfalfa organism. He identified the fungus as *R. Medicaginis* and thus established the greater importance of Rhizoctonia diseases, and greatly extended the

range of the fungus. He found a somewhat similar disease of the potato, but clearly distinguished the fungus as another species, as further indicated in another part of this paper.

Chief among those who extended our knowledge of the pathology and distribution of the violet root felt fungus was Rostrup ('86), who observed the fungus in Denmark and described its effects on various hosts.

EARLY TAXONOMIC AND MORPHOLOGICAL ACCOUNTS

The fungi belonging to the genus *Rhizoctonia* received attention taxonomically from the earliest mycologists. Brief references should be made to the works of some of those who have presented synopses of the genus or who have contributed to the solution of the problem regarding the taxonomic position of these fungi. Bulliard (1791) evidently based his description of species upon the observations and data of Du Hamel and de Bondaroy; emphasizing therefore the sclerotium as the fruit body, and believing it homologous with the truffle he gave to this fungus on *Crocus sativus* the name *Tuber parasiticum.* He contributed nothing further to the morphology of the species. Persoon (1801) did not accept Bulliard's disposition of the fungus, but named it *Sclerotium Crocorum,* and gave a diagnosis which, while based on the observations of the earlier writers, did not confuse the sclerotium with a true fruit body.

De Candolle (1815[a]), in his first taxonomic discussion employed Persoon's name for the fungus, and then, after giving the characteristics and parasitism of the species on alfalfa more careful attention, he established (1815, 1815[b]) the genus *Rhizoctonia* to include two species, *R. Crocorum* DC. on crocus and other hosts and *R. Medicaginis* DC. on alfalfa. It will be noted that he adopts Persoon's specific name for the crocus fungus. De Candolle also considers a doubtful species, *R. Mali,* reported on apple.

Nees (1816) placed the crocus fungus in *Thanatophytum* under the name *T. Crocorum.* Fries (1823) assigns *Rhizoctonia* to the *Sclerotiaceae* just following his extensive genus *Sclerotium.* It is important to note, since Fries' work has been

made the starting point for mycological nomenclature, that he designates three species in the following order, (1) *R. Crocorum* DC., (2) *R. Medicaginis* DC., and (3) *R. muscorum* Fr., also giving *R. Mali* DC. among *species ignota.* The descriptions of the two species first mentioned leave no doubt that he is here defining the violet root felt fungus of crocus and of alfalfa. Moreover, Fries recognized *Sclerotium Crocorum* Pers. as a synonym of *R. Crocorum* DC. So far as has been ascertained no specimens of these species which he examined are still in existence. Link (1824) excluded the doubtful forms, added a species *R. strobilina,* and otherwise left the genus as constituted by De Candolle. Duby (1830) included among the species *Rhizoctonia Allii* Graves, arranging the genus close to *Sclerotium* in the *Scleroteae* of *Lycoperdaceae.* Fries later included in this genus *R. Batatas* Fr. on *Ipomoea Batatas* from America.

The most complete mycological account of the genus *Rhizoctonia* is that given by L. and C. Tulasne ('62). They reduce *R. Crocorum* DC. and *R. Medicaginis* DC. to a single species to which they apply a new name, significant of the appearance of the fungus, *R. violacea* Tul. This reduction to a single form was made after a most careful morphological study of the fungus in all stages. From the accurate descriptions and the excellent illustrations it is clear that they had under consideration material referable to the names above. The Tulasne brothers also refer to other species insufficiently known, as follows: *R. Allii* Graves, *R. Batatas* Fr., and *R.* (?) *Mali* DC. They were inclined to the view that the affinities of the genus would be found to be with the *Ascomycetes,* and, in fact, they considered certain minute cushions of hyphae, referred to in detail later, as immature perithecia. Successively, therefore, attention was drawn by mycologists (1) to the sclerotium as a fruit body (Du Hamel and Bulliard), (2) to the sclerotium as a sterile structure (Persoon), (3) to the strand-like habit of the mycelium (De Candolle), and (4) to the minute cushion-like sclerotia as suggesting perithecia (Tulasne, L. and C.).

NAME, SYNONYMY, AND MATERIAL EXAMINED

Since the investigations of the brothers Tulasne many mycologists have studied the violet root felt fungus on its various hosts, especially on crocus, alfalfa, and certain root crops. There is general, though not complete, agreement in confirmation of the view that the crocus and the alfalfa forms are identical, and that this species, *R. Crocorum,* occurs on numerous hosts. I shall indicate later some of the morphological details in which the two forms agree and give other evidence supporting the view of a single species. For the present it is necessary to anticipate this evidence in order to state that until a perfect stage is definitely established, it would appear that the correct designation of the violet fungus is *Rhizoctonia Crocorum* (Pers.) DC. As noted above, the specific name applied by Persoon was adopted by De Candolle when he established the genus. This name, perhaps unfortunately, has priority over *R. Medicaginis* DC. in that it is mentioned first by Fries (1823). Though necessary, it may seem unwise to call the fungus *R. Crocorum,* inasmuch as it is far more widely distributed on alfalfa; and, furthermore, because its dicotyledonous hosts are more numerous. *R. violacea* would be a most appropriate descriptive name, but it is obvious that this also would not conform to the rules. The following provisional synonymy has been collated:

Tuber parasiticum Bull. (1791),
Sclerotium Crocorum Pers. (1801),
Rhizoctonia Crocorum DC. (1815),
Rhizoctonia Medicaginis DC. (1815),
Thanatophytum Crocorum Nees. (1816),
Tuber Croci Duby (1830),
Rhizoctonia Rubiae Dcne. (1837),
Rhizoctonia Dauci Rabenh. (1859),
Rhizoctonia violacea Tul. (1862),
Rhizoctonia Asparagi Fckl. [non Fr.] (1869),
Hypochnus violaceus Eriks. (1913).

The identity of *Rhizoctonia Crocorum* DC. and *R. Medicaginis* DC. suggested by the brothers Tulasne ('62) and accepted by most taxonomists, has been confirmed by a study

of all the material I have been able to examine, and there is included below a list of the material identified as *Rhizoctonia Crocorum* (Pers.) DC.

Exsiccati: *Rhizoctonia Medicaginis* DC., Linhart, Fung. Hung. Fasc. 4: *400; Rhizoctonia Dauci* Rabenh., Rabenhorst, Herb. Mycolog. Fasc. 1: *74.* (*Helminthosporium rhizoctonum* Rabenh.); *Rhizoctonia Solani* Kühn, De Thuemen, Myc. Univ. Cent. 18 : *1797.*

European collections: (1) Material from Prof. Delacroix, Paris, 1901, as follows: on sugar beet; on sugar beet, obtained by inoculation from diseased beet; on potato; on potato, by inoculation from affected beet; on crocus; on crocus, by inoculation from affected beet; on alfalfa; on *Onobrychis sativus;* on asparagus; and on asparagus, by inoculation from diseased beet. (2) On crocus from bulb gardens, Pithiviers, France, 1901. (3) From Prof. Aderhold, Proskau, Germany, 1899, on carrot and on root of young apple tree. (4) From Prof. Sorauer, Berlin, 1900, on potato and on asparagus. (5) From Herr Weigand, Helmitzheim, Bavaria, 1899, on alfalfa. (6) From Prof. v. Tubeuf, Munich, 1899, on sugar beet. (7) From Prof. Hartig, Munich, on roots of young conifer. (8) From Prof. Cugini, Modena, Italy, 1899, on alfalfa. (9) Material which the writer was able to obtain fresh near Munich, 1905, on sugar beet and alfalfa.

In 1901 the writer was unable to find in the Kew Herbarium or in Paris any type material, and none was found in Montpellier in 1905.

American collections: (1) From Mr. P. W. Graff, Manhattan, Kansas, 1911, on alfalfa. (2) From Mr. F. D. Bailey, Laurel, Oregon, (sent by Dr. G. L. Peltier, Univ. of Ill.) 1915, on potato.

DISTRIBUTION

In Europe the violet root felt fungus is in general widely distributed, but its occurrence now and then in epidemic form on some one host would appear to indicate some locality or race influence. On *Crocus sativus* the fungus has been reported from France chiefly; on asparagus, more frequently from France, Belgium, and Italy; on *Medicago sativa* it would

seem to occur more commonly from southern France eastward to Bavaria and Hungary and southward to the Mediterranean. No information is available with respect to its occurrence in Russia. On the fleshy root crops and on the potato the fungus has often been reported from central France and Germany northward through Denmark, Norway and Sweden, and also on the sugar beet in Italy. In Denmark it appears to be found oftener on species of *Trifolium* than on alfalfa.

The root felt disease is certainly not unknown to market gardeners and others throughout England, yet there are relatively few references to it in pathological literature. It would appear that Güssow has observed the fungus in England, for in speaking of diseased tubers from a farm in Essex he says, "They were covered with a dull reddish-brown webbing, which was raised into numerous points, as if grains of sand were below it," but in view of his reference in the same article to the commoner potato fungus no definite statement should be made. Salmon's account ('08) of the disease of seakale, described as "a felted mass of violet spawn or mycelium," evidently refers to this species.

In the United States *R. Crocorum* was first reported from Nebraska by Webber ('90) on lucerne. He states that it was rare in the Nebraska flora at that time. Heald ('06) lists the fungus as among disease-producing organisms prevalent in Nebraska during 1905. The record is as follows: "Root rot. *Rhizoctonia violacea* Tul. reported from a single locality: Platte County. Not common in that region." The complete observations made in 1906 were not reported until later, in which account, however, Heald ('11) fails to make note of Webber's earlier report of its occurrence. Freeman ('08) refers to the fungus as the cause of a well established disease of alfalfa in Kansas, and a specimen received by the writer in 1911 from that state indicates that it is identical with the European fungus. More recently it has been mentioned by Gandara ('10), and the inference is that it is found on alfalfa in Mexico. The first occurrence on potato in America is from a locality in Oregon (Bailey, '15). No well authenticated instance of the occurrence of this fungus in South America,

Australia, Asia, or Africa has come to my attention, yet the distribution of alfalfa growing throughout the world and the frequent interchange of seed might suggest that the distribution of the organism may be found to be much more general than is reported. It should be mentioned that Shaw ('13) reports the fungus from India, but he has obviously been misled regarding the fungus concerned, as will be shown later.

Du Hamel represented the violet root fungus as prevailing under a variety of soil conditions, but electing dry, gravelly, and acid localities. It is reported by the brothers Tulasne that while wet weather may give the fungus an advantage, still it is found in the driest situations permitting crop growth. In central Germany Kühn's studies led to the suggestion that on root crops and potatoes it is found more frequently in low and stagnant places. Frank and Comes concur in this view. The writer was able to observe the fungus in the vicinity of Munich in 1905 and in the fields examined, it was found under conditions which appeared to be favorable for the growth of the host. The very general occurrence of the fungus in southern Europe, especially in southern France and Italy, would seem to indicate that excessive moisture is not always an important factor. At the same time the fungus is of frequent occurrence in Scandinavia. It is not reported as one of the more serious diseases of any host in England. In the more humid regions of the eastern United States it is unknown, while two of the localities from which it has been reported are regions of lower humidity and lesser rainfall.

HOST PLANTS AND GENERAL SYMPTOMS

There is every reason to believe that the number of host plants for *Rhizoctonia Crocorum* is much greater than has been reported. The fungus has been observed upon many economic plants; and it has been reported in the agricultural press of Europe as occurring upon a variety of weeds, but these references are not always definite. Eriksson has made some observations regarding the plants attacked when culti-

vated in soil from a carrot field known to be infected, and the following weed hosts are noted: *Stellaria media, Myosotis arvensis, Galeopsis Tetrahit, Erysimum cheiranthoides, Urtica dioica.*

This would indicate that a careful study of any epidemic would confirm the view that the number of hosts is considerable. The following is a list by families of the host plants which have been reported in the more accessible literature:

Pinaceae
- Abies pectinata
- Picea alba
- Picea excelsor
- Pinus Laricio
- Pinus montana

Liliaceae
- Asparagus officinalis
- Crocus sativus
- Lilium sp.
- Muscari sp.
- Narcissus sp.
- Tulipa sp.

Urticaceae
- Ficus silvatica
- Humulus Lupulus
- Urtica dioica

Polygonaceae
- Rumex crispus

Chenopodiaceae
- Beta vulgaris
- Chenopodium album

Caryophyllaceae
- Spergula arvensis
- Stellaria media

Cruciferae
- Brassica campestris
- Brassica Rapa
- Crambe maritima

Rosaceae
- Crataegus oxyacantha
- Pyrus Malus

Leguminosae
- Anthyllis vulneraria
- Coronilla varia
- Medicago lupulina
- Medicago sativa
- Melilotus alba

Leguminosae
- Onobrychis sativa
- Ononis spinosa
- Ornithopus sativus
- Phaseolus sp.
- Trifolium hybridum
- Trifolium pratense
- Trifolium repens
- Vicia Faba

Geraniaceae
- Geranium pusillum

Rutaceae
- Citrus Aurantium

Vitaceae
- Vitis sp.

Umbelliferae
- Daucus Carota
- Erysimum cheiranthoides
- Foeniculum vulgare
- Pastinaca sativa

Oleaceae
- Ligustrum vulgare

Convolvulaceae
- Convolvulus arvensis

Boraginaceae
- Myosotis arvensis

Labiatae
- Galeopsis Tetrahit

Solanaceae
- Solanum tuberosum

Rubiaceae
- Rubia tinctoria

Caprifoliaceae
- Sambucus Ebulus

Compositae
- Taraxacum officinale
- Sonchus arvensis
- Sonchus oleraceus

The difficulty in giving an accurate list of hosts compiled from the literature is, however, a serious one, since one cannot be certain that all the observations are carefully made. Again, some mycologists do not distinguish the two species of *Rhizoctonia* here discussed; thus Salmon ('08), after describing an interesting disease of seakale with all the characteristics of *R. Crocorum,* goes on to refer to carnation stem rot, damping off, and other diseases as if they were induced by the same fungus, doubtless, however, intended to have reference to another related fungus.

Regarding the above-ground symptoms of affected plants, it may be said that they are not striking, and were it not for the characteristic dead area in the field it would not be an easy matter to designate slightly affected plants. Generally, there is in alfalfa evidence of yellowing, sometimes marked chlorosis, while in beets and carrots there is merely a paler appearance of the foliage, followed by wilting. The critical period for affected alfalfa is usually about the time of the second cutting, and at this time considerable wilting may occur without preliminary indications of lack of health. In these main effects the disease is remarkably similar to the Texas root rot of cotton, alfalfa, and other plants. The unmistakable symptom is the relatively sudden dying of the plant affected.

The disease is generally though not necessarily fatal. Even a plant so susceptible as the alfalfa may recover from early injuries, usually with the loss of the tap root. Under certain conditions the disease incites the development of adventitious roots,—which may be a factor in recovery. The progress of the disease in the field is radial, and during the first year especially, circular dead areas mark its presence. The spread of the fungus during the season may be from a few feet to several rods. After the first year or two, considerable areas irregular in outline may be involved.

MYCELIUM AND SCLEROTIA

It would be difficult to confuse the mycelium of the violet root felt fungus with any other species, for when one is

familiar with it in the different stages of development it is at all times an organism with striking characteristics. Such differences in appearance as may be found in comparable stages on the various hosts may be regarded as causally related to the host substratum, or, at least they may be so regarded until adequate morphological differences or contrasting physiological relations are established. The general appearance of affected roots of asparagus, carrot, beet, or alfalfa are well expressed in some of the common names applied, such as red root, root felt disease, violet fungus, etc.

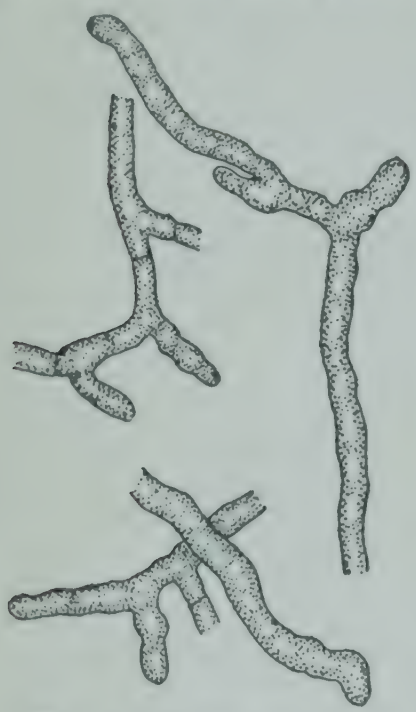

Fig. 1. *Rhizoctonia Crocorum:* Young hyphae.

With sufficient time for abundant growth the fungus completely invests the root or root system with a mantle, weft, or mat of hyphae of characteristic color. In the early stages of growth on the root the mycelium is pale buff to violaceous, but when the root is completely invested, the mycelium is red-violet to violet-brown, and always violet-brown with age or when densely matted. The numerous small darker papillae or "minute sclerotia" in the mantle of mycelium are in reality cushion-like mycelial bodies described later.

In the following description the writer will not attempt to follow all changes in the development of the various mycelial conditions, but will endeavor to give briefly those developmental features of greatest interest and those diagnostic characteristics which may be applied to most herbarium material. For further morphological details the accounts of L. and C. Tulasne ('62) and Prillieux ('91) should be consulted.

The external, general hyphae are more or less different in form and appearance with age. The younger hyphae are usually dilutely violaceous with a pigment which may be decolorized by the application of acidulated water. The pro-

toplasm is dense towards the tips of branches and vacuolated farther away. The hyphae are somewhat flexuous, branched (sometimes closely), with the branches arising at right angles to the main hypha, and with a partition wall laid down at not over 10 μ distant (fig. 1). With age the hyphae become rigid, somewhat less in diameter, 4–8 μ, the branching is distant, and these branches readily break off at the first partition wall (fig. 2). At the point of union the diameter is uniform with the main hypha. The partition walls are distant,

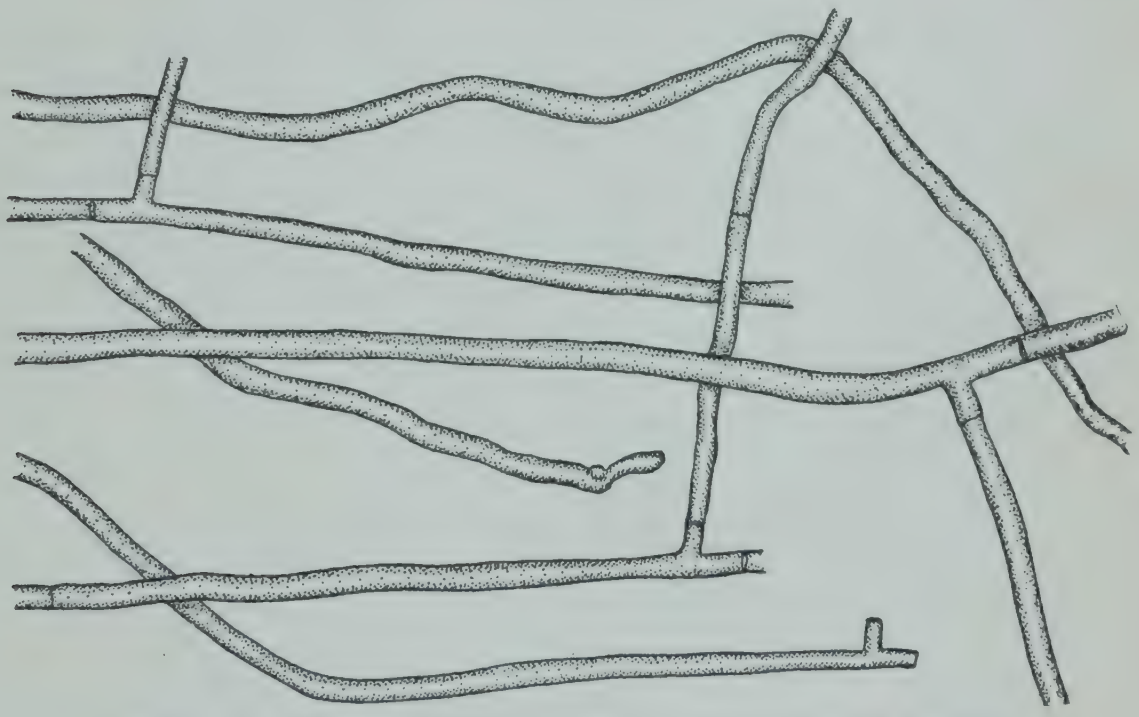

Fig. 2. *Rhizoctonia Crocorum:* Mature root-investing hyphae.

often 120–200 μ apart. The walls now possess the violet-brown pigment and in the lumen little or no protoplasm is observable.

The internal mycelium is likewise branched, septate, often associated into loose strands, passing between the cells or traversing them. In the early stages of the disease, so far as reported, these internal hyphae are nearly colorless; Prunet reports that there are sometimes areas of brown mycelium in the attacked tissues, and this I find particularly true of asparagus. The internal hyphae are generally of less diameter than those constituting the external mat.

Disregarding for the time the small cushions already men-

tioned, the hyphae constituting the external mantle may be uniformly distributed, as is the case usually when the fungus attacks fleshy roots or tubers, or they may also form a number of aggregates having the appearance of loose or root-like strands. The strands are developed later rather than early in the progress of the disease. They are conspicuous on such hosts as alfalfa and sainfoin. These strands course along the whole root system; they also pass out into the soil, apparently beyond the minutest rootlets, and doubtless attack plants in the vicinity. Upon the larger strands sclerotia may be formed, and thus the sclerotia are connected with the mantle of hyphae.

Infection Cushions.—Small stromatic bodies distributed amongst the hyphae were noted by several of the early observers. Kühn ('58) calls special attention to them on the carrot and the potato. The brothers Tulasne ('62) studied and described them in some detail and came to the conclusion that these were the early stages in the development of the perithecial form. Search for the reproductive phase was in this way transferred from the sclerotium to the bodies in question. Sorauer ('86) among others accepted the view of the perithecial nature of this structure. Prillieux ('91) seems to have been the first to point out that the "corps miliaires," as he termed them, are in reality special mycelial cushions having the important function of effecting the penetration of the host. He regarded them as the main, if not the sole, seats of tissue invasion, and his studies included a comparison of these bodies and of the penetrating strands in alfalfa, sugar beet, and crocus. After mentioning these cushions as one type of sclerotia, Prunet designates them more specifically as minute "corps noirâtres," .2 to 1.2 mm. in diameter with a brown hyphal cortex and a colorless medullar. He indicates that these as well as the larger sclerotia send out filaments which enter the soil and extend the fungus. These bodies have also been figured by Bailey ('15) in the case of the occurrence of the fungus on the potato in Oregon and particularly well by Salmon and Crompton ('08, pl. 25). The writer is of the opinion that Prillieux's notion is in general correct,

and while they are not the only means of penetration they are most important in this connection.

The hosts upon which the writer has had the opportunity to examine the infection cushions in best condition are alfalfa, carrot, and asparagus. The cushions are distributed over infected roots, often 1 mm. apart in alfalfa, .5 mm. in carrot, and 3 mm. in asparagus. The external hyphae are for the most part similar to those of the general mycelium, but there occur also branches in which the cells are short and swollen, sometimes resembling a short chain of spores. This form of hypha may have given the suggestion of a conidial stage (see Kühn ('58), Sorauer ('86), and others. The medullary portion of younger cushions is made up of finer, almost colorless hyphae, and it is this type which enters—strand-like—the cortical tissues of the root, destroying particularly the cambium and younger phloem regions. In the later stages of development it will be found that the cushions seem to extend considerably into the cortex, and more of the hyphae are colored.

In this connection it is well to call attention briefly to some gross changes in the affected roots. By the time the host (alfalfa) reaches the critical stage, the bark slips readily from the root. The disintegration may continue further, however, through the spread of the fungus to the medullary rays and all other parenchyma, so that the root shreds or crumbles when lifted. The late stages of destruction may be assisted by saprophytic organisms. It is difficult to determine if the fungus continues its growth for a short time after the death of the root. At any rate, the fungus rapidly disappears with the further decay of the roots.

In the case of asparagus the cushions are largely superficial and the main affected tissues are beneath the shell of thick-walled cells constituting the periphery of the host. In the carrot the invading strands are large, and the host cells in the vicinity rapidly collapse and darken. I have been fortunate in obtaining affected asparagus roots at intervals after the disease had run its course. In no case could any evidences of spore forms be found which gave promise of genetic connection. On the contrary, the fungus gradually disappears,

first the mantle of mycelium, and then the cushions, so that when the root is reduced to a mere shell there are only vestiges of the cushions remaining.

Sclerotia.—The true sclerotia are flattened or rounded bodies varying in diameter from a few millimeters to several centimeters. When mature they are of a deep violet-brown

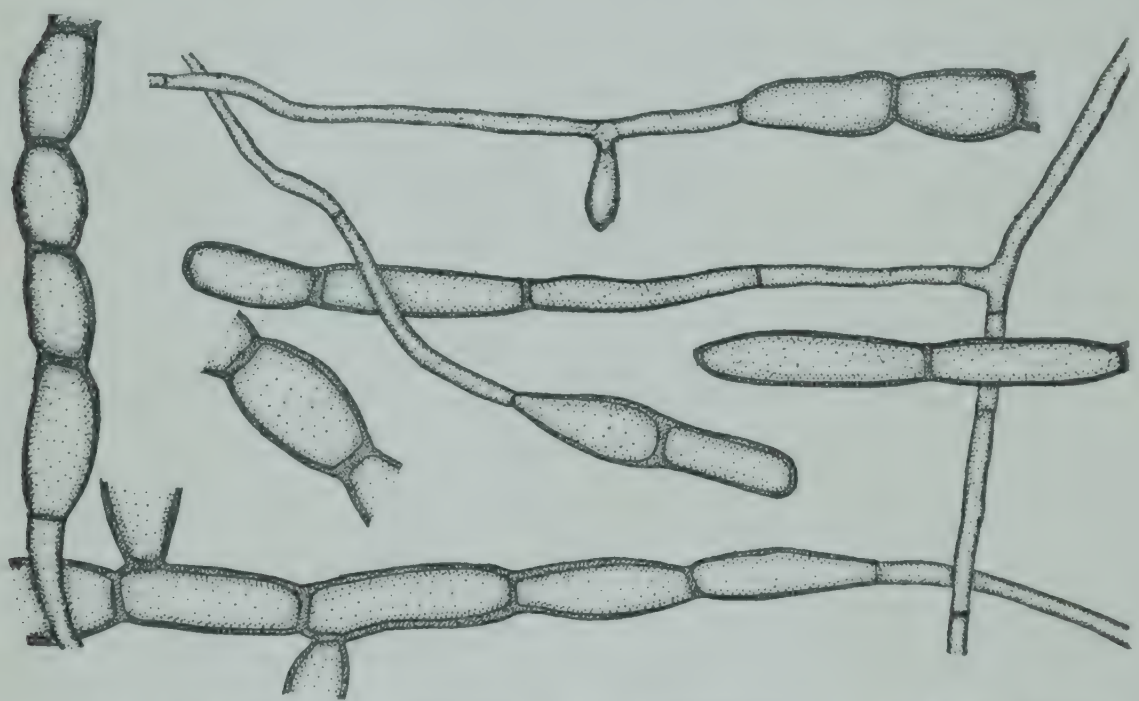

Fig. 3. *Rhizoctonia Crocorum:* Cells characteristic of the tufted growth covering the surfaces of the large sclerotia and to a certain extent of the "infection cushions."

and are thickly clothed with a persistent velvety felt, externally of the same color as the root-investing hyphae, but darkening further in. Among the surface hyphae of the sclerotia as well as of the "infection cushions" are found chains of enlarged cells (fig. 3) quite distinct from the enlarged cells of *R. Solani.* The sclerotia, as noted previously, are always connected with the root felt by large hyphal strands. In the saffron disease the sclerotia are formed both in contact with the shriveling bulb and also in the adjacent soil. On affected alfalfa roots they often occur below, and in the angles of, the larger branches, but often one finds no sclerotia in immediate contact with the host. In connection with diseased carrots, beets, and potatoes, they are not so frequent, unless perhaps they are then formed at greater

distances from the plant. Most herbarium material, unfortunately, with the exception of crocus specimens, does not include sclerotia.

In section a sclerotium consists of fairly compact tissue made up of cells often considerably branched and sometimes curiously lobed (fig. 4).

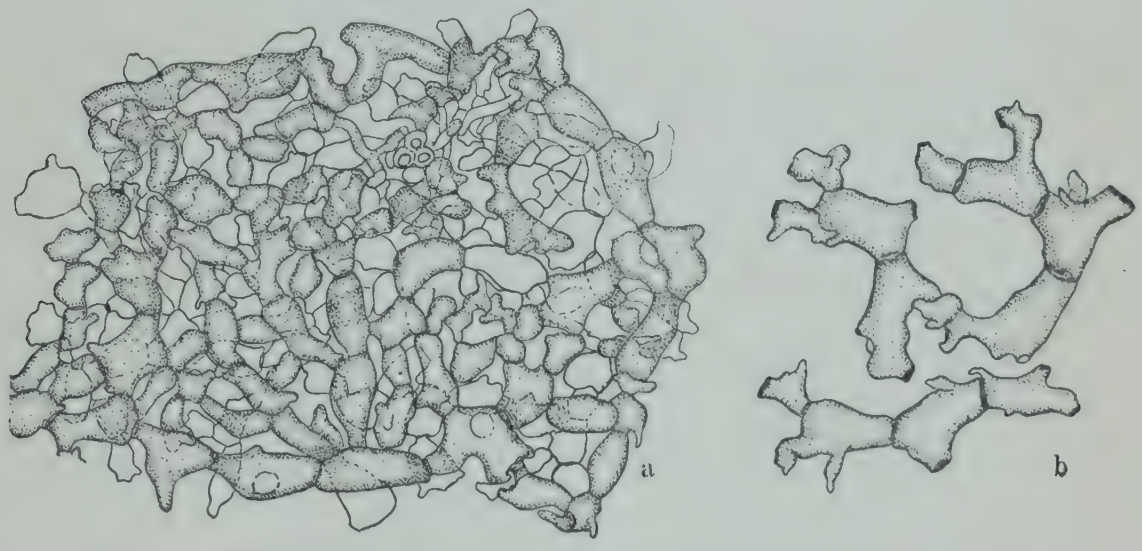

Fig. 4. *Rhizoctonia Crocorum:* a, from a section of a large sclerotium; b, extreme forms of cells isolated from a macerated sclerotium.

SUGGESTIONS REGARDING THE PERFECT STAGE

It has been noted that Du Hamel and other early observers stated that the affinities of the violet fungus were with the truffles. Persoon, Fries, and others placed the genus near *Sclerotium.* Tulasne considered the small sclerotia as probably a stage in the development of an ascomycete (pyrenomycete). This suggestion of Tulasne has apparently influenced many mycologists, and a search in this direction for the perfect stage has continued practically until the present time. Fuckel suggested that *Lanosa nivalis* Fr. might be considered the first or conidial stage of this fungus and he believed that the minute sclerotia or penetration cushions gave rise during the latter part of the season to pycnidia. With the more complete disintegration of the affected tissues he reported the development of a perithecial stage, and this fungus he called *Byssothecium circinans* (*Leptosphaeria circinans* (Fckl.) Sacc., *Trematosphaeria circinans* (Fckl.) Wint.). It will be noted that Winter regarded this

view of the genetic relation to *Rhizoctonia* as improbable; and Saccardo, who at first accepted the relationship, subsequently changed his opinion. Prunet ('93) states that he made certain inoculation experiments from which he was convinced that Fuckel was correct; but we possess no indications as to how these experiments were conducted. The writer in 1899, at Leipzig, germinated the spores of *Leptosphaeria circinans* and obtained a mycelium bearing no resemblance to the Rhizoctonia hyphae. The idea that *Leptosphaeria* constitutes a perfect stage of the *Rhizoctonia* has had no support recently, although Comes ('91) incorporates it in an extreme form in his treatment of the genus.

Rostrup ('86) found in the spring on the old roots of affected plants a pycnidial stage which he considered to be connected with the Rhizoctonia hyphae; and on the old roots of *Ligustrum* he found reddish filaments and scattering perithecia; the latter he identified as a species of *Trichosphaeria.* His assumption, however, has received no encouragement. When Hartig ('80) discovered a *Rosellinia* as the perfect stage of his *Rhizoctonia Quercina* there was a temporary revival of interest in the quest for one of the *Ascomycetes* as the perfect stage of *R. Crocorum.*

Frank ('97) reported observing the violet fungus on the grape, and associated with it he found a species of the *Thelephoraceae.* This he regarded as the perfect stage, and to the fungus he applied the name *Thelephora Rhizoctoniae.* This observation has failed of confirmation.

Eriksson ('13) has recently presented an extension of his earlier account ('03[a]) of diseases produced by *Rhizoctonia,* and in this he records a new "*Hypochnus,*" *H. violaceus* (Tul.) Eriks. as the perfect stage of "*Rhizoctonia violacea,* Tul." In this he was stimulated by the observations of Rolfs ('03) and others in America, and Pethybridge ('11) in Ireland, on the occurrence of the basidial stage (*Corticium vagum* B. & C. or *Hypochnus Solani* Prill. & Del.) of *Rhizoctonia Solani* Kühn, resulting in a reëxamination of some material of the violet fungus on roots and stems of certain wild plants. This material had been preserved in alcohol thirteen

years earlier. The result of his study is reported as follows:

> "D'après ces renseignements, il faut—du moins pour ce qui concerne les formes du champignon qui envahissent les Carrottes—considérer comme résolue la question tant débattue de savoir à quel groupe rapporter le mycélium stérile connu sous le nom de *Rhizoctonia violacea.* Dans ce qui suit, je vais indiquer le nom scientifique qu'il faut donner, ainsi que les caractères diagnostiques du champignon autant que j'aie pu en juger sur les documents conservés que j'avais à ma disposition."

On the basis of these observations he creates the *Hypochnus* mentioned. No adequate diagnosis is given, but the important part of the account is as follows:

> "Ensuite le champignon forme autour des tiges de la même plante ou d'autres espèces de plantes immèdiatement au-dessus du sol, une enveloppe annulaire, membraneuse, d'un rose tendre, qui, montant souvent sur les tiges jusquà une hauteur de 5 à 15 mm. et s'étalant parfois sur la surface du sol comme une feuille toute mince, produit des basidiospores. C'est le stade *Hypochnus.*"

This apparently refers to material on *Stellaria media, Myosotis arvensis, Galeopsis Tetrahit, Erysimum cheiranthoides, Urtica dioica,* and *Sonchus arvensis,* which hosts he would regard as harboring the Hypochnus stage of that form of the violet fungus attacking the carrot, and for this reason the names just given appear in the list of hosts.

In the writer's opinion he properly considers it remarkable that the fructification stage should attack hosts other than those producing the sterile stage. In view of the character of the material, the incompleteness of the account, and the possibility of confusion with *Corticium vagum* B. & C. it would appear necessary to await confirmation of the observation that a *Corticium* (*Hypochnus*) may represent the perfect stage of the fungus here discussed, although, reasoning from the apparent relationship of this species to *R. Solani,* a Corticium stage might well be assumed. The writer has been unable thus far to secure any of the material mentioned.

In a footnote Eriksson expresses himself thus: "Quant à la Rhizoctone de la Luzerne, je suis porté à croire, d'après les

observations de cette année (1912), quelle doit être rapportée à un groupe d'Ascomycètes." This suggestion is both interesting and surprising since Eriksson adopts the Tulasnes' name for the *Rhizoctonia* on carrot and this would seem to concede the identity of the carrot and alfalfa forms. It is also in a measure inconsistent with his inoculation results, as reported later.[1]

CROSS INOCULATION AND CULTURAL STUDIES

The amount of cross inoculation work yet reported is not considerable, and for this, doubtless, the inability to cultivate the organism is largely responsible. Throughout the early literature numerous indications are offered showing that following a severe outbreak of the disease on any crop, it may appear on susceptible plants grown in the affected area—observations which tend to establish the identity of the fungus on different hosts. Among later observations may be mentioned those of Güntz ('99) who records that in a field where alfalfa and red clover had been seriously affected, beans, potatoes, and tuberous artichokes were planted; the potatoes subsequently developed the disease in serious form, and the other plants showed indications of its presence. In England it is reported (Bd. of Agr., '06) that potatoes are affected by the violet felt fungus, especially when following alfalfa; and under similar conditions the fungus appears upon clover, carrots, beets, and mangolds.

Eriksson ('13) undertook some cross inoculation work employing, in zinc cylinders, soil from diseased carrot fields (eight cylinders) in contrast with soil taken from areas free from the disease (two cylinders). At the same time, to the diseased soil he added pieces of carrots affected by the fungus. The cylinders were permitted to stand over winter

[1] Since obtaining proof of this paper I have received from Prof. Eriksson an advance reprint of his paper, "Fortgesetze Studien über Rhizoctonia violacea DC." Arkiv för Bot. 14 (Art 12) : 1–31. *f. 1–13.* 1915. It is impracticable to include here a full discussion of this paper. It is necessary to state, however, that he treats at length *Rhizoctonia Medicaginis* DC. and *R. Asparagi* Fckl., and includes inoculation experiments indicating form differences. After germinating the spores of *Leptosphaeria circinans* he comes to the conclusion that, in spite of his earlier work on *Hypochnus violaceus*, the pyrenomycete mentioned is the perfect stage of *R. Medicaginis*. Prof. Eriksson has also furnished material of *R. Asparagi* and of the *Leptosphaeria*.

and the following spring were planted to several varieties of carrots, to beets, mangolds, red clover, and alfalfa. At the time of harvest, the carrots were all more or less severely affected, while the sugar beets and alfalfa showed very light attacks, and the clover none at all. Continuing the work in subsequent seasons he obtained evidence in one case—that of the sugar beet—pointing to an increased virulence of the fungus with adjustment to that host. On the contrary, in the second year the alfalfa exhibited greater resistance, thus rendering a decision as to the existence of physiological races hazardous. He also reported, that on placing diseased soil and diseased carrots in a box in which various weeds were permitted to grow, the fungus appeared on eight species of weeds (representing several families), apparently a considerable proportion of those present. This also would seem to discourage the idea of marked host specialization.

Attempts to cultivate the violet fungus on artificial media have been made by several investigators without success. While in Leipzig, 1900, I obtained particularly good material on alfalfa from Bavaria. Dilution cultures were attempted both on various kinds of agar and on gelatin, but no growth of the fungus was secured in any case. Further trials were made with material from France in 1902, and again upon receiving comparatively fresh material from Kansas in 1911. Bailey ('15) reports an endeavor to cultivate the organism in Oregon, also without success. It is quite possible that special conditions are essential to its growth in artificial culture, but we should not assume that it is incapable of growth in this way. It would appear that the presence of contaminating organisms is not the sole cause of the difficulty, since isolated hyphae in the dilution cultures remain free from the growth of contaminating organisms, and yet themselves fail to develop a colony of growth. It will be recalled that Atkinson[1] found difficulty, but ultimate success, in growing *Ozonium omnivorum* (Lk.) Shear, the cause of the southwestern root rot of cotton. The writer also found that this organism is not readily cultured, but obtained a satisfactory

[1] Bot. Gaz. **18**: 16–19. 1893.

growth on cotton decoction starch paste in 1902. Since in general pathology and physiology the cotton *Ozonium* and the violet *Rhizoctonia* have much in common, a further careful investigation of their life relations would doubtless yield interesting results.

PREVENTION AND CONTROL

Relief measures respecting the violet fungus are very largely limited to the practices of good culture, good drainage, and sanitation. The early pathologists have generally recommended pulling up diseased plants and burning them. It is well to point out, however, that after a careful examination of the distribution of the fungus on the smallest fibrous roots, it has been found to invest these to a considerable depth in the case of alfalfa, and therefore a very small measure of security may be expected unless one carries out this recommendation in a far more thorough manner than is practicable in the field. The further suggestion has been made that where the diseased areas are few, small, and clearly defined, trenches may be dug to prevent the further spread of the disease; but if this should prove feasible under any conditions, it would be advisable only in connection with a thorough disinfection of the isolated areas by formaldehyde or sulphuric acid—the former disappearing from soil in time, and the latter being easily neutralized by liming. The rotation of crops is undoubtedly desirable, but complete immunity from the disease cannot be expected if we may trust the statements of Du Hamel and other observers to the effect that the fungus may remain alive in the soil for periods of from three to twenty years. The fact that many hosts are affected also complicates the practice of rotation.

The Common Rhizoctonia, R. Solani Kühn (Corticium vagum B. & C.)

EARLY STAGES

In addition to his discussion of the violet *Rhizoctonia* on beets and carrots Kühn ('58) described a disease of potatoes, of which the causal organism was recognized as a species of

Rhizoctonia differing notably from the violet organism, and to this potato fungus he gave the name *R. Solani.* The life history of the fungus and the symptoms of the disease induced were very imperfectly known at the time, so that the description could not be complete. As a result, those who subsequently discussed the genus *Rhizoctonia* have sometimes recognized *R. Solani,* while others have referred the organism to *R. Crocorum* (*R. violacea*), and still others have assumed that *R. Solani* Kühn was also the cause of another disease of beets and of carrots mentioned by Kühn without identifying the causal organisms. After a study of certain diseases in America induced by *Rhizoctonia,* I was keenly aware of this confusion, so when opportunity presented itself in the winter of 1899–1900 I conferred with Professor Kühn regarding those diseases, and also endeavored to obtain satisfactory specimens of the fungi. There has been no earlier opportunity to utilize the information obtained in connection with a general discussion of the genus.

Kühn laid special stress upon a scab ("Schorf oder Grind," later termed "Pockenkrankheit") of potatoes, sometimes followed by deeper seated injuries and decomposition ("als Räude und Krätze bezeichnet"). The symptoms are clearly those that we now know as one type (cf. McAlpine, '12) of the potato diseases ascribed to *R. Solani* Kühn (*Corticium vagum* B. & C.). It has been noted that the fungus was not so well described as might be wished, and the spores mentioned were evidently those of contaminating organisms, or else the oval cells of the tufted stage of the fungus; but when we use in connection with this general description Kühn's comparison of this plant with the violet fungus (Kühn, '58, p. 248) it is convincing that the fungus on the potato which he had under consideration was not *Rhizoctonia Crocorum.*

The sclerotia were also inadequately described and figured. With reference to that point, however, Professor Kühn stated that while a common form of the fungus on the tubers consisted of irregular superficial sclerotia, this form did not lead to serious consequences and therefore received less attention from him. Material of this superficial sclerotial stage was

furnished the writer by Professor Sorauer in 1900 (for a photograph see Duggar, '09, p. 477, fig. 219), and, subsequently, from other points in Germany. It is clearly the "black speck" form of the disease now generally recognized. Professor Kühn also identified cultures of the American fungus on sugar beets (Duggar, '99) as very close to, if not identical with, his *R. Solani.* In 1858 Kühn was obviously unaware of the fact that the violet fungus also occurs on potato in Germany; and, in fact, he told me in 1900 that it was subsequent to 1858 when he first collected specimens of the violet fungus on this host. "The violet fungus produces no serious epidemics of the potato in Germany," he declared. Professor Kühn was unable to locate type material of *R. Solani,* and such material is doubtless unavailable. Before presenting still other indications pointing unmistakably to their identity, I shall proceed on the basis that it is correct to refer the sterile stages of the commoner American *Rhizoctonia* on potato and other plants to *R. Solani* Kühn, and once studied comparatively there can be no confusion of this plant with *R. Crocorum* (Pers.) DC.

A disease of carrots was also described by Kühn with which no fungus was positively associated. The indications are insufficient to determine whether this was a fungus or a bacterial disease. So far as the writer is aware no disease of carrots in Europe due to *R. Solani* has since been reported, though in 1900 Professor Kühn stated as his opinion that carrots as well as beets in Germany were affected by a fungus similar to *R. Solani.*

The violet root felt fungus was clearly distinguished by Kühn ('58, see pp. 235–237, 243–249) in its occurrence on both beets and carrots. It is not possible to mistake his statements in which the organism on these hosts is referred to *Rhizoctonia Medicaginis* DC." Moreover, he nowhere suggests the combinations *R. Dauci* Kühn and *R. Betae* Kühn, which later crept into the literature of the subject. This fact makes it difficult to understand the nomenclature employed by Eidam ('87) and Comes ('91). In discussing a beet disease prevalent in Germany, Eidam refers the organism to *Rhizoctonia Betae* Kühn. He gives a description of the disease and of the fun-

gus, including its growth on culture media. It is clearly the beet disease now well known in America, and of which the causal fungus is referred to *R. Solani.*

Kühn did describe the symptoms of another disease of beets, and this last bears every indication of being the heart rot later known to be due to *Phoma Betae* (*Phyllosticta tabifica*), much discussed by Frank and others. Kühn's discussion of this other beet disease has been interpreted, also, in the way I have indicated by Prillieux and Delacroix ('91) and others outside of Germany. In my conference with him, Professor Kühn stated that the only Rhizoctonia diseases of beets and carrots which he knew in the vicinity of Halle in 1858 and earlier were those due to the violet fungus, and of these he exhibited specimens having the usual characteristics. From the evidence at hand, therefore, the Rhizoctonia disease of beets described by Eidam was new on that host. It would seem, then, that Eidam is the authority for the combination *R. Betae,* which he attributes to Kühn. In any case it becomes a synonym of *R. Solani* Kühn (*Corticium vagum* B. & C.).

In discussing the Rhizoctonia disease of potatoes in Europe Sorauer ('86) describes unmistakably the "black speck" or sclerotial form of the fungus, and while he, like many others, assumed that it would be found to belong among the *Ascomycetes,* it is obvious that the characteristics of this stage of Kühn's fungus were well recognized.

Among the forms of *Rhizoctonia* which he enumerated and discussed Comes ('91) includes *R. Dauci* Kühn, and *R. Betae* Kühn. In his discussion of the first-named he reviews Kühn's account of the violet fungus on carrots, already mentioned; but in the account of *R. Betae* Kühn he evidently refers both to Kühn's account of the heart rot of beets and to the Rhizoctonia disease of this host described by Eidam. Pammel ('91) was the first American pathologist to report in this country a disease now known to be caused by *R. Solani.* He, however, followed Comes and Eidam in referring to the fungus causing the beet rot as *R. Betae* Kühn.

Atkinson ('92, '95) studied a "sterile" fungus causing sore

shin or damping off in cotton, and ascertained that the same fungus was commonly associated with, and capable of, inducing damping off of various seedlings in the greenhouse.

Duggar ('99) also referred to the beet rot fungus in America as *Rhizoctonia Betae* Kühn, following Comes, and was able to determine that this beet fungus was identical morphologically (mycelium and sclerotia) with the damping off fungus found by Atkinson. The characteristics of the two organisms in culture were also identical, both forming on certain media a rich mycelium and finally numerous flaky or tufted centers of growth, some of which become irregular, often crust-like, sclerotia. Neither on affected seedlings nor on beets were sclerotia ordinarily produced (compare, however, Edson, '15, pl. 23).

Subsequently, Duggar and Stewart ('01) reported that several types of disease, on a variety of hosts, including the potato, were induced by *Rhizoctonia.* The account given was intended to be merely preliminary, and for this reason a few words of explanation are necessary. The account referred to did not (perhaps unfortunately) explicitly indicate that, as far as the studies had progressed, there was evidence that the organism, or forms of the organism (except in the case of the form on rhubarb, referred to later) exhibited morphologically and in culture the characters of the beet rot and damping off fungus. The authors were likewise convinced, after a study of European material of Kühn's fungus on the potato, of the identity of the American and European forms on this host. Cultural studies were being carried forward with *Rhizoctonia Solani* from many hosts, since there was the possibility of establishing definite forms or races, of finding the perfect stage, and of discovering other species. Again, specimens of the violet root felt fungus on various hosts had been obtained by one of us, and it was intended to include in a final paper a general account of the genus.

This failure to designate the form with which we worked has doubtless led to some misunderstanding (see Prillieux '97, Eriksson '13, p. 17). However, in a more recent account (Duggar, '09, pp. 477–478), it will be seen that the diseases

discussed are ascribed to *R. Solani* (*Corticium vagum* B. & C.).

DISTRIBUTION

Rhizoctonia Solani is distributed throughout the United States and Canada. There is every reason to believe that it exists as a saprophyte in most arable soils, and under certain conditions may attack many species of plants. It is perhaps most frequently noted as a damping off disease in greenhouses and seed beds, but this occurrence may be explained by the fact that here the conditions are probably more conducive to the pathogenicity of the fungus. On the potato it is likewise wide-spread, although, as noted later, the economic importance of the diseases induced varies in different sections of the country, probably in accordance with climatic and soil conditions. In all potato-producing states and regions it is a well-known disease. On the sugar beet it has been observed in many states. The fact that it is an important disease of one crop or another in every section of the country is alone sufficient indication of its general occurrence. *Rhizoctonia* has been mentioned in Brazil by Potel ('00), but it is not clear to which species he refers.

It is rather surprising to find that *R. Solani* has received relatively little attention in Europe. Although recognized as inducing a disease of the potato widely distributed in central Europe, and occasionally reported on the beet, yet little careful work has been bestowed upon the fungus. Eriksson ('13), seems to be unfamiliar with the fungus in Sweden. On this account we can gain no incidental information regarding *R. Solani* as a result of his extensive studies of the related species in that country. The following will express his attitude regarding *R. Solani:*

> "Il paraît très douteux, du moins si l'on en juge d'après les descriptions et les figures données, que les nouvelles formes de la Rhizoctone stérile signalées dans ces derniers temps par B. M. Duggar et F. C. Stewart sur une quantité de plantes différentes en Amérique (* * *) soient vraiment identiques aux formes du *Rhizoctonia violacea* qui ravage l'Europe."

We have very little data regarding its occurrence in other sections of continental Europe, although from conference

with Prof. Delacroix in Paris (Nov. 28, 1901) and from an examination of material furnished by him I learned that it is not uncommon throughout France on the potato. It will be recalled that the perfect stage was described by Prillieux and Delacroix ('91). Judging from the amount of the black speck disease observed on the potato in the markets of various cities in southern Europe during 1905–'06 the writer would infer that it is of more frequent occurrence than is reported. Pethybridge ('11) finds the fungus (including the Corticium stage) well distributed in Ireland, and it is reported from other parts of Great Britain.

McAlpine ('11) has reported this fungus on the potato from several points in Australia, and he states that it occurs upon a variety of economic plants. Since it has proved a serious disease in very few localities, it receives little attention, and is therefore freely disseminated by commercial intercourse. It is also known in New Zealand and Japan.

The investigations of Shaw ('13) suggest that *Rhizoctonia Solani* may be an important disease-inducing organism in some of the more humid regions of India. Reference is made later (pp. 448–450) to the fact that he has obviously misapplied this name, however, and also that other confusion has resulted. In spite of this, it seems certain that he has observed all stages of the fungus.

TYPES OF DISEASES INDUCED, SYMPTOMS

It is not my purpose to attempt a complete description of the more important diseases caused by this species, yet sufficient will be included to indicate the main types of diseases thus far investigated, their general distribution, and their striking pathological relations. By types of disease, I have reference to general effects or symptoms. The effect of the fungus upon the stems may occasion a different appearance from its action upon the root, and thus there arise the different types referred to. With respect to penetration and action upon the cell the behavior of the fungus may be the same in all cases. Moreover, as a result of the primary injury, secondary effects may occur, and sometimes such secondary phe-

nomena may be so striking in appearance as to dominate the primary injuries or lesions.

For convenience we may arrange the types of disease in the following categories: (1) damping off, (2) stem rot, (3) root rot, (4) leaf rot, (5) scab, and (6) such secondary effects as rosette, little potato, and leaf roll. Since more than one type of disease may occur upon a single host, and especially since one form of the disease may grade into another, it will be more practicable to discuss these under the following captions: (1) damping off, (2) potato diseases, (3) rot of fleshy roots, (4) stem and root rots of herbaceous plants, and (5) fruit and leaf injuries.

DAMPING OFF

It would appear that the first mention of a disease of seedlings caused by *Rhizoctonia* is that of beets, recorded by Eidam ('87), although he gives no complete account of the evidence. It is preferable to date our knowledge of damping off diseases caused by *Rhizoctonia* from the work of Atkinson ('92), who studied particularly sore shin of cotton, but he also found the "sterile" fungus to cause damping off of seedling beets, radish, lettuce, egg plants, cabbage, and other plants in the forcing house. The later identification of the fungus concerned (Duggar, '99) and its association with the damping off of various plants (Duggar and Stewart, '01) was only the beginning of the observations which have now served to direct our attention to the vast importance of this fungous disease throughout the United States both in the greenhouse and in the outside seed bed.

Among numerous instances in which damping off has been reported due (or in all probability due) to this fungus may be noted the following: (1). It has been found as a source of serious injury to ginseng in the seed bed (Van Hook, '04; Whetzel and Rosenbaum, '12). (2). Tobacco seedlings are so frequently injured that soil treatment has received special consideration in the case of this crop (Selby, '04; Cook and Horne, '05). (3). As a damping off disease of cotton (sore shin) it occurs not only in America but in Africa (Balls, '05, '06) and possibly in India (Shaw, '13) as well. (4). Tomato

seedlings seldom attacked by *Pythium* have been found to succumb to *Rhizoctonia* in Louisiana (Edgerton and Moreland, '13). (5). Alfalfa seedlings have been reported susceptible in one instance (Stewart, French, and Wilson, '08). (6). Seedlings of various species of conifers from a few days to nine weeks old have been reported attacked in several instances (Hartley, '12, Clinton, '13).

The majority of the instances reported above were under normal seed bed or field conditions. Many other cases of the damping off of seedlings might be included where seeds are grown in crowded condition in moist greenhouses. Again, damping off of cuttings by *Rhizoctonia* is now a well-known phenomenon in the propagating house, and special precautions are taken with respect to drainage and moisture in order to reduce the injuries to a minimum. It is safe to assume—since the fungus seems to be found in practically all soils—that it is in general the worst enemy of seedling plants. In fact, it may be anticipated that under conditions favorable for the fungus the damping off of seedlings of numerous species may be anticipated. So far as the writer has been able to ascertain there has been no report of the damping off of monocotyledonous plants under normal seed bed conditions.

While *Rhizoctonia Solani* may perhaps induce damping off in innumerable species regarding which observations are lacking, some of the host plants which have come to the writer's attention as particularly susceptible are the following: lettuce (*Lactuca sativa*), celery (*Apium graveolens*), beet (*Beta vulgaris*), cress (*Lepidium sativum*), tobacco (*Nicotiana Tabacum*), balsam (*Impatiens balsamina*), snapdragon (*Antirrhinum majus*), cotton (*Gossypium* spp.), cucumber (*Cucumis sativus*), squash (*Cucurbita* spp.), sunflower (*Helianthus annuus*), carrot (*Daucus Carota*), radish (*Raphanus sativus*), and phlox (*Phlox Drummondii*).

Since the phycomycetous damping off fungus *Pythium* has been known to pathologists much longer, and prior to 1895 was practically the only fungus to which this type of disease was ascribed, it is probable that much damage due to *Rhizoctonia* has been ascribed to *Pythium*. Moreover, unless

examined microscopically, there are no symptomatic differences between the effects of the two organisms.

Seedlings affected exhibit symptoms somewhat different with age. The youngest seedlings of all delicate plants show what may be called the usual damping off characteristics. Near the base of the stem an hygrophorus or translucent appearance is quickly followed by shrinkage of the tissues and weakness of the stem. The plants topple over, the fungus invades all parts, and spreads rapidly to the neighboring individuals. The cells of the sap-perfused tissues are flaccid and injured, some showing this even before the entrance of the hyphae into the cells. Somewhat older plants and the more robust seedlings of cotton, bean, etc., often exhibit characteristic lesions. Atkinson ('95) gives a description of its effect on cotton seedlings as follows:

> "The trouble is caused by the fungus growing first in the superficial tissues of the stem near the ground and disintegrating them before it passes to the deeper tissues; in other words the fungus never seems to penetrate far in the living tissues, but 'kills as it goes,' and the tissues become brown, depressed, and present the appearance of the plant having a deep and ugly ulcer at the surface of the ground. The fungus does not spread into the tissues either above or below the ulcer to any extent, but literally eats away at that point until it has severed the stem at the affected place or the plant has recovered from its effects."

DISEASES OF POTATOES

The potato is the most interesting of the host plants with respect to the parasitism of *Rhizoctonia* by reason of the many types of disease induced under diverse conditions. The conditions may be in part climatic and, in part perhaps, dependent upon the pathogenicity of the particular strain of the fungus or upon the stage and development of the host at the time of infection. It has been noted that when Kühn first described the disease of potatoes in Germany he laid emphasis upon a scab which was often followed or accompanied by decay. This form of the disease was probably less prevalent in the country as a whole at that time, and the more recent accounts indicate that the "black speck scab" or "black speck," properly the sclerotial stage, is the feature by which the main type

of the disease is now generally known. At present the following main types of injury are recognized for the potato: (1) black speck scab or sclerotial stage, (2) Rhizoctonia scab, (3) Rhizoctonia rot, (4) stem lesions and root rot, (5) rosette and leaf roll, and (6) little potato and aerial potato.

Black speck is a form of the disease most widely distributed and in itself scarcely merits consideration as a "disease" at all, since the sclerotia are superficial on the tuber, and it is merely the appearance of the potato which is affected. The sclerotia may lead to other types of disease which are more serious. The black specks show up most clearly when the potatoes are wet and it is only at this time that they present the appearance of being black, for, as indicated later, the normal color of the sclerotia is deep brown. It was this form of the disease which first gave evidence of the wide distribution of the fungus in America (Duggar and Stewart, '01), and it has been shown to exist in practically all potato-producing sections of the United States and Canada. It occurs throughout Europe, especially on the later varieties of potatoes. It is also reported from India, Africa, and Australia, so that it may be assumed to be world-wide in its distribution on this host. It is safe to say that this is the only form of the disease which does not result directly in serious injury and loss to the crop. In the United States, especially from Ohio westward, other forms of the potato disease assume a seriousness nowhere else attained. If all such forms of the disease mentioned below occur in the Atlantic states they are of little consequence. They are, moreover, far less frequent in Europe, India, and Australia.

The Rhizoctonia scab is believed to occur as a result of the penetration of hyphae during the early stages of sclerotial development, and occasionally it may be induced by a late growth of new hyphae from old sclerotia. The writer has had an opportunity of examining only casually this form of the disease. It is one of the types doubtless seen by Kühn. According to McAlpine ('11), when this disease occurs, practically every part of the tuber is affected, no normal skin remaining. In severe cases the scab areas may be thrown into folds or puckers and these rub off easily in the form of "cork dust."

It is reported that the irritating hyphae are then found at the bases of such scab formations. This scab has been reported fairly common in Europe and in Australia. Güssow ('05) seems to refer to the same type in England, and Rolfs ('03) describes it from Colorado. Specific scabs of the potato have been clearly defined and related to particular organisms. The capacity of the tuber to respond with cork formation to varied injuries suggests that in certain modifications of Rhizoctonia scab this fungus may accompany other active scab inducing agents.

The Rhizoctonia rot is a form of disease which appears relatively late in the season when certain conditions prevail, or possibly when the fungus has for one reason or another developed unusual virulence. The disease is supposed to originate either from stem infections, from sclerotia, or from scab areas. In any case penetration of the mycelium occurs to a considerable depth, and according to McAlpine ('11) there is produced in Tasmania a form of the disease known as brown rust, characterized in the early stages by dark spots in the tuber resembling certain symptoms of *Phytophthora.* It may also be associated more or less with the deeper form of the Rhizoctonia scab. During the latter part of the season a typical stem rot may occur which is not characterized by the definite lesions described later. Instead, the affected cortex slips readily from the wood and about the bark a considerable web of the yellow-brown hyphae may be found superficially, below and just at the surface of the ground, and the pith may be fairly stuffed with the mycelium. Plants only slightly affected with this form of the disease, especially when growing on rich garden or muck soil, have been found to yield the collar or *Corticium* stage.

It is not always easy to distinguish as separate forms of the disease, stem lesions, rosette, little potato, aerial potato, rolling, etc., for these types of injury are often associated. All of these types except stem lesions are properly secondary effects, and there is abundant evidence that all represent responses of the plant to disturbed condition or nutrition, sometimes associated with native weakness. It would not be

strange, therefore, if somewhat similar effects should characterize, as they do, purely "physiological" disturbances. Stem lesions are generally dark, sunken areas, clearly different from black leg, occurring at the surface of the ground or on any of the underground stems, or tuber-forming stolons. These lesions may result in the early death of the affected plants. Selby ('02, '03) maintains that generally the lesions upon young shoots are associated with stunted growth and the production of rosette-like clusters of the upper leaves, as well as with less marked modifications of habit, including slight leaf rolling. Drayton ('15) finds the hyphae in the lesions.

If the tuber-bearing stolons are the seat of injury, the food supply is cut off from the young tubers and there may result "little potato," a form of the disease which Rolfs ('04) has found to be an important cause of the potato failures in Colorado. Little potato in Australia is considered an evidence of underground injuries occurring late in the season. Injuries which effectually girdle the stem, especially if these occur during a moist season or when the crop is frequently irrigated, lead to the formation of aerial tubers. In the relation of *Rhizoctonia* to the various types of potato diseases much remains to be investigated, and Orton ('14) rightly suggests that inadequate attention has been bestowed upon the question of the predisposition of the tubers used as seed, since it is quite possible that these may yield offspring with tendencies toward rosetting, leaf rolling, and other morphological modifications.

ROT OF FLESHY ROOTS

The root rot of beet, apparently first described by Eidam ('87) in Germany, and shortly afterward found by Pammel ('91) in Iowa, was observed in New York (Duggar, '99) some years later. Since that time it has appeared epidemically in Nebraska (Lyon and Wianco, '02) and other western states. The fungus is most virulent during midsummer or later. Infection may take place at the bases of the leaves or on the fleshy root. The leaf bases blacken, the leaves become paler, and finally wilt. Pammel ('91) has drawn attention to the

fact that when fleshy root crops of this type are attacked by such fungi they die gradually, while herbaceous plants (cotton, alfalfa, etc.) wilt suddenly. This is probably closely related to the effect of the fungus on the conducting tissues. In the beet root the invaded tissues are pale brown, and often cracks or rifts occur, though rotting may take place without such lesions. Sometimes there is partial recovery after the cracks are formed, and in this case callous tissue is developed.

A soft crown rot of the radish induced by this fungus has apparently been reported only once (Duggar and Stewart, '01). A similar disease of the carrot was found in 1900 in New York and this is possibly the disease first reported by Kühn ('58, pp. 241–243), although he did not identify it as due to a *Rhizoctonia*.

STEM AND ROOT ROTS OF HERBACEOUS PLANTS

Rhizoctonia Solani produces serious stem and root rots of a number of economic herbaceous plants, among which the following are known to be important: carnation (*Dianthus caryophyllus*), Sweet William (*Dianthus barbatus*), bean (*Phaseolus vulgaris*), sweet-pea (*Lathyrus odoratus*), and violet (*Viola odorata*).

The carnation stem rot is one of the most destructive diseases occurring on this host and is wide-spread in the United States. The general symptoms of the disease on carnation and Sweet William are much the same. The stem is affected at or just below the soil level. The fungus penetrates and kills the cortex which may be readily slipped from the wood. Through the medullary rays the hyphae also enter the pith, which likewise decays. In later stages of the disease the wood shreds, due to the complete penetration by the fungus of all parenchymatic tissues.

Several important epidemics of *Rhizoctonia* on bean have been reported from different parts of the United States. In addition to the outbreak described by Duggar and Stewart ('01), Hedgcock ('04), a few years later, found the bean disease severe near St. Louis. The base of the stem and the larger roots bore characteristic ulcerations; pods were af-

fected, and through the sunken areas of these the hyphae penetrated the seed and produced small sclerotia on the seed-coats. The fungus was cultivated and typical Rhizoctonia hyphae and sclerotia were obtained. Fulton ('08) observed the disease in Louisiana on stems and pods, with the characteristic ulcerations, especially at the surface of the soil or just below. He proved the causal relation of the organism through cultures, and inoculations yielded positive results with the damping off of seedlings. McCready ('10) reported the bean disease as new to Ontario, where it was also characterized by stem and pod ulcers. In New York Barrus ('10) observed an epidemic of this host in which as many as 30 per cent of the plants were affected. He determined the fungus by cultural studies and proved its pathogenicity by inoculation. On the sweet-pea the disease is mainly a root rot, yet the base of the stem may also be considerably affected before the plant succumbs. On the violet it is primarily a crown disease, but where the plants are succulent and the conditions are moist, the leaves are considerably invaded.

FRUIT AND LEAF INJURIES

In discussing stem diseases the occurrence of *Rhizoctonia* on bean pods has been mentioned. Another case of fruit injury is described by Wolf ('14), who found a severe rot of egg plant fruits from which the fungus was obtained. The pathogenicity of the organism was determined by inoculations, and cross inoculation from tomato and potato led to the conviction that the organism was *Rhizoctonia Solani.*

Direct attacks of leaves by *Rhizoctonia Solani* are infrequent. From the habits of the fungus this would be expected. The one serious leaf disease reported is that of lettuce (Stone and Smith, '00), in which the fungus spreads over the whole surface, causing a moist rot. Sclerotia are frequently formed in connection with this affection. It would be anticipated, perhaps, that diseases of a similar nature might be found on other plants with the rosette habit. Leaf stalks are frequently invaded, or may be the regions of first attack, in the case of the beet disease. The disease of leaf stalks of rhubarb

reported by Duggar and Stewart ('01) is not due to typical *R. Solani.*

MYCELIUM AND SCLEROTIA

The morphological characteristics of the hyphae and sclerotia have been adequately described by several writers, but it may be well to summarize some of the more important features. Upon such hosts as the potato, sugar beet, carnation, and others there is more or less development of an external web, but never over the general root system such a complete investment of roots by a mantle of hyphae as characterizes the violet fungus. The external hyphae are somewhat colored, usually yellowish brown, and they are generally of two types. One type may be designated as purely vegetative and another as constituting the external tufts or masses when these occur. All hyphae are practically colorless when young, vacuolate, more or less irregular, septate with the septa at intervals of 100–200 μ. The diameter of vegetative hyphae is 8–12 μ. Branches arise, and when young these are inclined in the direction of growth and are invariably somewhat constricted at the point of union with the main hyphae (fig. 5). As the hyphae mature and become more deeply colored they are more uniform and rigid, the distances between cross walls are greater, the constrictions where branches arise less marked, and the branches are approximately at right angles to the main hypha.

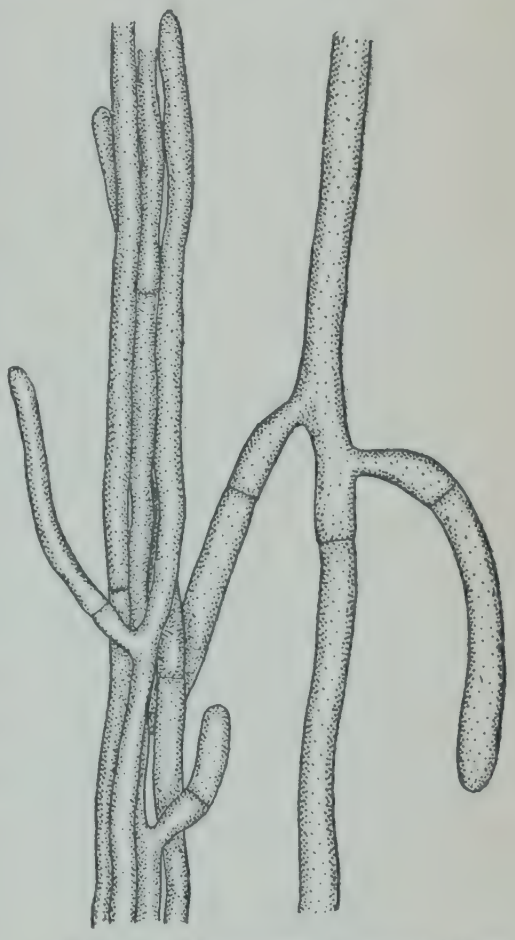

Fig. 5. *Rhizoctonia Solani* (*Corticium vagum*): A vegetative hypha and a small strand from artificial culture on potato.

On certain affected plants a short tufted or mealy growth occurs and this is made up of hyphae of very different characteristics. In the young condition threads are profusely

branched and lobed, sometimes botryoid, and they are ultimately divided into short, ovate cells, arranged in short chains, or elbowed, and producing branches in a more or less dichotomous fashion (figs. 7 and 8). In culture the denser

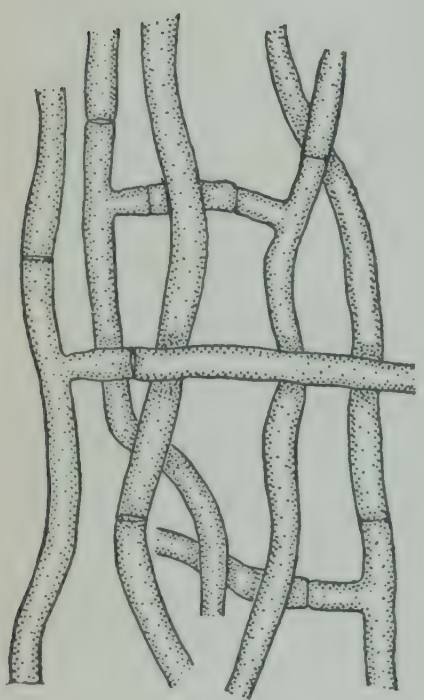

Fig. 6. *Rhizoctonia Solani:* Vegetative hyphae.

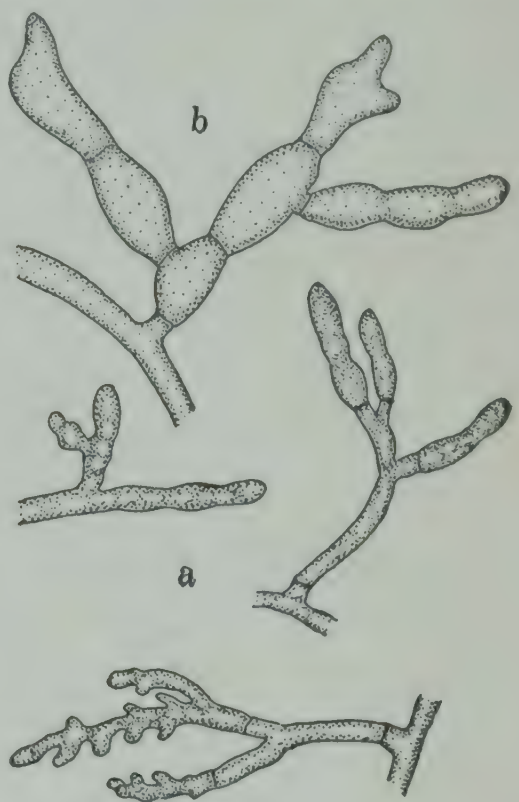

Fig. 7. *Rhizoctonia Solani:* a, young hyphae from young sclerotial tuft on lettuce; b, older cells from same source.

masses give rise to sclerotia. With maturity these hyphae become light brown in color, they break up readily into short hyphal lengths or single cells, the individuals of which bear some resemblance to conidia. However, they could not easily be mistaken for spores, although they may function as such, inasmuch as most of them may germinate within a few hours when placed under suitable conditions. I have previously described ('99) this process as follows:

> "So far as observed, germination is always by the protrusion of a tube through a septum. When several cells are connected, a germ tube from one cell may pass into and through its neighbor, * * * *, and thus peculiar appearances may result. Some of the cells of the hyphal chains seem to be devoid of protoplasm, and from neighboring protoplasmic cells the germ

tubes seem to pass into such empty cells as readily as directly into the nutrient solution. When the germ tube is from 10 μ to 20 μ in length, it is invariably narrowed towards the outlet from the parent cell, and a septum forms at a short distance from this outlet."

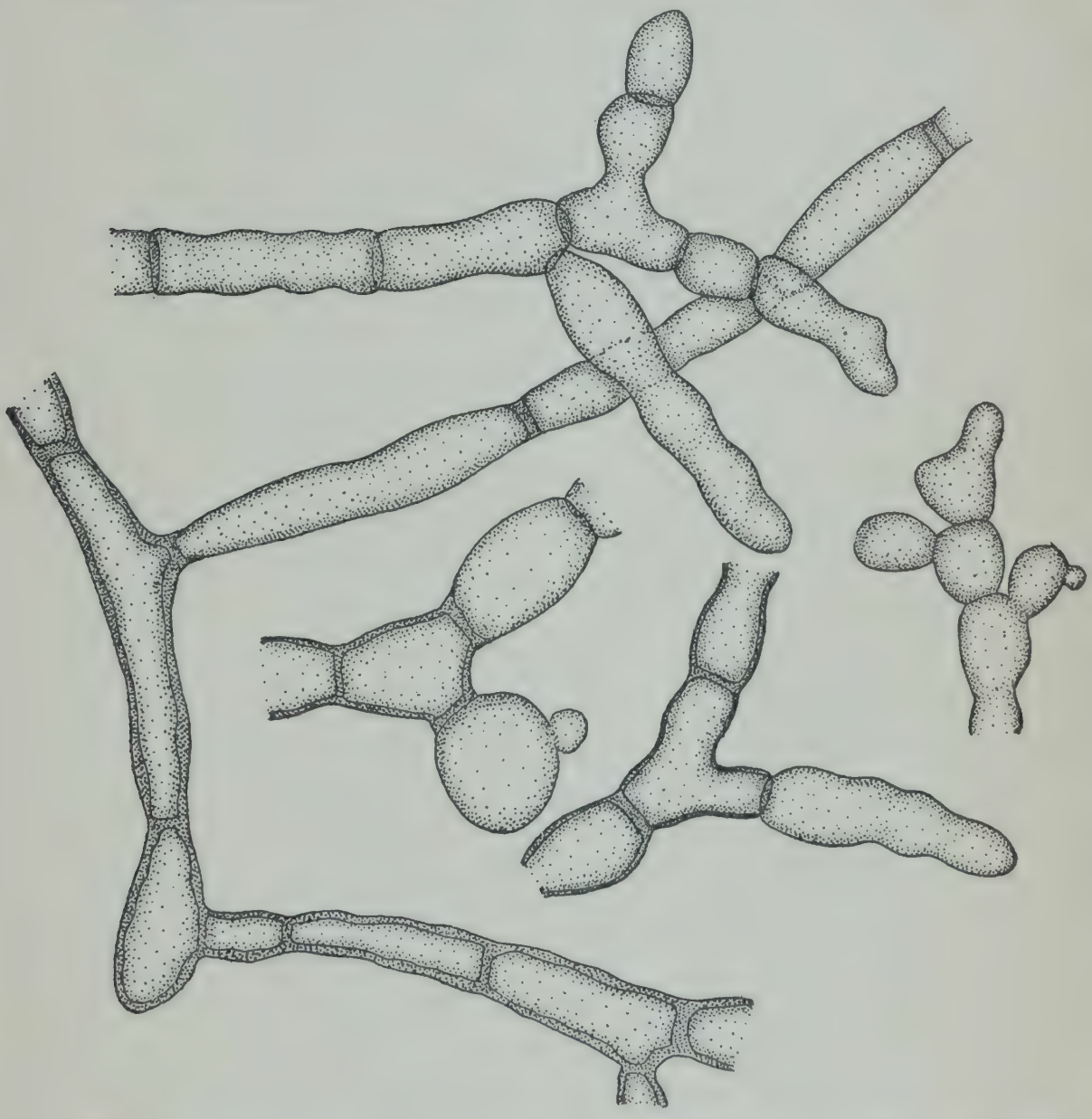

Fig. 8. *Rhizoctonia Solani:* Lobulate, moniliform, and elbowed cells from tufted growth in artificial culture.

The hyphae which penetrate the tissues remain colorless so long as they are in active growth, and while generally less in diameter they present much the same appearance as the young external hyphae. In the different strains which have been studied, originating from different hosts, certain minor modifications of the general habit of the fungus in culture have been observed. But these have not seemed to be suffi-

cient to be considered of specific importance, except in the case of the form on the rhubarb. In general, the differences referred to consist in a variable amount of the mealy or tufted growth, or of the amount of aerial growth; differences in the color of the colony are also observable; and the rapidity with which sclerotia are formed are all minor distinguishing features. The subject needs further investigation, but in general it is felt that these differences are such as might be due to permanent differences in the pathological strains, on the one hand, or may be regarded as temporary differences due to the recent environment, on the other. It may be pointed out that the appearance of the mycelium of the beet fungus from the damping off seedlings is not exactly comparable with that of the mycelium derived from the beet rot. When the organisms from both sources are grown in culture they are found to be identical. Strains do occur, however, evidence of which may persist for some time in the general appearance of the cultures.

The exact conditions under which sclerotia may occur on the various hosts affected have not been determined. It has been noted that affected potato tubers are the main seats of sclerotia formation when the fungus attacks that host. Upon this plant they are typical, and the numerous illustrations published are sufficient evidence that the appearance is much the same under a variety of conditions. Special attention may be called to the illustrations of Duggar and Stewart ('01), Rolfs ('02), Duggar ('09), McAlpine ('11), Pethybridge ('11), and Morse and Shapovalow ('14). On the majority of hosts, however, sclerotial formation is relatively rare.

From the various illustrations referred to it will be seen that the sclerotia vary in size from those so minute as to be scarcely visible, to others which may be a centimeter or two in diameter. They are generally more or less flattened, irregular, deep chestnut-brown, and generally smooth on the surface (that is, free from a looser growth of investing hyphae). Smoothness of sclerotia, which has been regarded by Kühn as of much diagnostic value, should not be considered

an important character except under natural conditions. Sclerotia which develop on fleshy organs in moist chambers as well as those which develop in culture show to a certain degree, a semi-persistent hyphal investment; but such investing hyphae are readily worn away, whereas in the violet fungus they are truly persistent.

Sections of the denser sclerotia exhibit a fairly homogeneous structure (fig. 9), with the cells more uniform in size and appearance than in *Rhizoctonia Crocorum.*

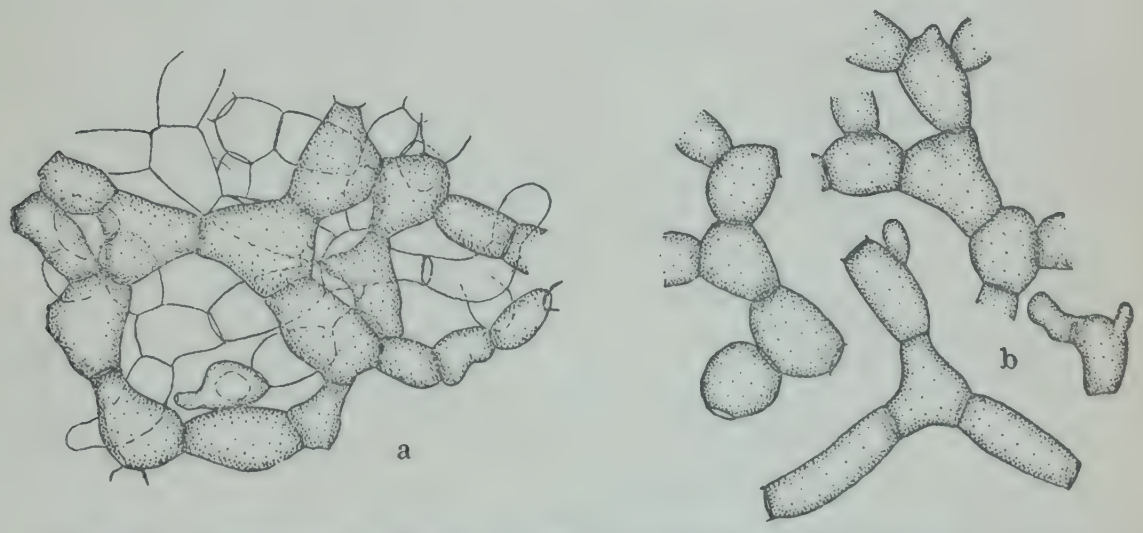

Fig. 9. *Rhizoctonia Solani:* a, from a section of sclerotium on potato; b, cells isolated by maceration of sclerotium.

THE BASIDIOSPORE STAGE, SYNONOMY, AND MATERIAL EXAMINED

Besides suggestions of a general nature no indications regarding the perfect stage of *Rhizoctonia Solani* were made prior to the discovery of the *Corticium.* Prillieux and Delacroix ('91) described *Hypochnus Solani* from potato stems, and although at this time the Rhizoctonia diseases were known in Europe no connection with this Hypochnus stage was suspected. The characteristic collar of mycelium was found surrounding the stem just above the surface of the ground, but they found nothing to indicate that the fungus had injured particularly the plant affected.

Rolfs ('03) found the collar fungus during his studies of potato diseases in Colorado. The material was determined by Prof. E. A. Burt as referable to the species *Corticium vagum* B. & C. On account of the parasitic habit, however,

it was considered advisable to make the fungus a variety of the Berkeley and Curtis species, so that it was written *Corticium vagum* B. & C. var. *Solani* Burt. Prof. Burt also recognized that it agreed closely with, and might be identical with, *Hypochnus Solani* Prill. & Del. This conclusion the writer accepts, but in view of the fact that Professor Burt is preparing a monograph of the *Thelephoraceae,* I shall not discuss this point; for the same reason I need only express doubt regarding the validity of Shaw's suggestion that *Hypochnus ochroleucus* Noack and *Corticium vagum* B. & C. are identical, although there is a certain similarity in the various stages.

Rolfs ('04) was able to germinate the basidiospores and to develop characteristic Rhizoctonia hyphae from these. Riehm ('11) also reported germinating the basidiospores and producing a characteristic Rhizoctonia mycelium together with the formation of sclerotia. Pethybridge ('15) gives a more complete account of mycelial production from spores.

The herbarium and fresh material which has been examined and found to agree with the authentic descriptions of *Rhizoctonia Solani* Kühn (*Corticium vagum* B. & C.) may be briefly enumerated:

Exsiccati: *Rhizoctonia Napaeae* nov. sp., Westendorp and Wallays, Herb. Crypt. Fasc. 5: *225.* (On decaying turnips which had been stored in a cave.)

American material: Hyphal stages on numerous hosts, many of which are mentioned in this paper, also others not included; sclerotia, on potatoes grown throughout the eastern and central United States, on potato stems (New York, 1900), on bean pods (New York, 1910), also on carnation stems, lettuce leaves, etc. Corticium stage from Prof. F. H. Rolfs, Colorado, 1901, on potato stems; from Dr. I. C. Jagger, Rochester, New York, 1914, on potato stems and on crown of carrot; from herbarium of Prof. E. A Burt, material on moist soil and decayed wood, collected by Prof. Farlow, Magnolia, Mass., 1903; from Herb. Mo. Bot. Garden, Nos. 44679, 44681, and 44682; collected by Dr. Geo. L. Peltier, Urbana, Ill., 1915.

European material: Sclerotia on potato tubers from Prof.

Sorauer, Berlin, 1900; from Prof. Magnus, Berlin, 1901; from Prof. Delacroix, Paris, 1901; and material secured on the markets of various cities, 1905–06.

As far as the writer has been able to determine, the following synonomy may be listed for *Corticium vagum* B. & C.:

Rhizoctonia Solani Kühn (1858).
Rhizoctonia Betae Eidam [non Kühn] (1887).
Rhizoctonia Napaeae West. (1846).
Rhizoctonia Rapae West. (1852).
Hypochnus Solani Prill. & Del. (1891).

PREVENTION AND CONTROL

Much the same situation confronts us regarding the prevention and control of *Rhizoctonia Solani* as in the case of *R. Crocorum.* The presence of the fungus in practically all soils serves to emphasize the importance of cultural methods including drainage and sanitation. In this case, however, since the fungus is of so much importance in the seed bed and in the greenhouse special preventive measures may be practised. Selby ('06) found that the treatment of the seed bed with formalin (1:160 to 1:200) proved satisfactory in most cases. In general, the best results have been obtained by steam sterilization, and where the facilities are at hand it is practicable to apply this to any type of greenhouse work, and, in certain cases, to seed beds outside. Liming has been recommended for the control of the disease in the field, but this has not been uniformly successful, and cultural studies have shown that the fungus is able to withstand a high percentage of alkalinity. Nevertheless, when liming results in the improvement of physical and sanitary conditions of the soil it undoubtedly assists in restraining the activity of the fungus in an indirect way, possibly by raising the resistance of the host.

Even though the fungus may be widely distributed, it is advantageous to plant clean "seed." This applies particularly to the case of the potato. The presence of the sclerotia upon the tuber makes possible the early spread of the fungus

to the young shoots. It has been positively determined that the more effective tuber treatment is the standard corrosive sublimate solution, as for potato scab. In all cases, however, it would be better to employ seed which are not infected, if this is possible.

Conclusions and Notes

In the account already given of *Rhizoctonia Crocorum* perhaps sufficient discussion of the occurrence and the characteristics of this form has been entered upon, except in the way of a direct comparison between this species and *R. Solani,* subsequently included. Further work upon the first named species should consider especially the culture of this organism, inoculation experiments, the development of the organism as it occurs on several hosts, the formation of sclerotia and infection cushions, and the confirmation or more definite declination of Eriksson's view that the fungus is referable to *Corticium* (*Hypochnus*). From the study of this organism thus far the following conclusions seem justified:

1. The views of L. and C. Tulasne that the forms of *Rhizoctonia* on crocus, alfalfa, and other hosts may be included in a single morphological species is confirmed.

2. The correct name of the violet root felt fungus, so long as a spore stage remains uncertain, is *Rhizoctonia Crocorum* (Pers.) DC.

3. This organism occurs throughout a considerable part of Europe and has been found in a few localities in America.

4. It attacks a variety of plants representing many families, mostly dicotyledonous.

5. The mycelium and sclerotia exhibit no important differences in equivalent stages on the different hosts, but large sclerotia which form freely in contact with crocus, and often near the affected roots of alfalfa, are seldom observed in connection with the attacks upon beets, carrots, and some other hosts.

6. The existence of distinct forms or races of this species requires further extended study.

7. The organism has not yet proved culturable with the usual laboratory methods.

8. At the present time there is insufficient evidence to determine what the perfect stage of this organism may be.

Obviously much still remains to be done regarding the physiological, pathological, and taxonomic relationship of the culturable forms which in the vegetative stage may be referred to the form-genus *Rhizoctonia*. The writer has grown in culture *Rhizoctonia* from twenty-three different American hosts, most of which are mentioned by Duggar and Stewart ('01). Most of these were grown upon a variety of culture media including prune juice, beet, and potato agar; also beans, stems and pods, celery, sugar beet and potato cylinders, and corn meal mush. With one exception (the organism from rhubarb) the cultural characteristics have been sufficiently similar, especially after protracted culture in the laboratory, to suggest a single species, with characteristics of the beet and cotton fungus, already sufficiently described (Atkinson, '92, '95; Duggar, '99). Moreover, these cultural studies have confirmed in all cases the conclusions tentatively arrived at from the preliminary microscopic examination of the fungus on the different hosts. Reasons have already been given to indicate why this species is properly *R. Solani*. It is recognized, however, that much culture and inoculation work is necessary to establish the point that the fungus on the various hosts is the same species, and to determine to what extent physiological forms may occur.

The following brief summary of conclusions may be presented with regard to *Rhizoctonia Solani:*

1. The common American species of *Rhizoctonia* is *R. Solani* Kühn.

2. This fungus is widely distributed in America and elsewhere, and would seem to occur on the potato in most regions of the world where this crop is a staple product.

3. The host plants represent many families of dicotyledons, *Asparagus Sprengeri* being the only monocotyledonous host thus far reported.

4. The types of disease induced are most diverse, damping off and root and stem rots being the most important direct effects. Secondary effects have been studied only in a few localities.

5. The mycelium and the sclerotia, as well as the general appearance on the host, readily distinguish the fungus from *Rhizoctonia Crocorum* (Pers.) DC.

6. The organism is readily culturable by the usual laboratory methods.

7. The evidence seems clear that the perfect stage of this organism is *Corticium vagum* B. & C.

It is to be regretted that the fungus causing a disease of rhubarb (Duggar and Stewart, '01) was lost before adequate study could be bestowed upon it. The fungus bore a close resemblance to *Rhizoctonia,* but the aerial hyphal cells were shorter and of greater diameter than those of *R. Solani.* No sclerotia were found on the host, and they did not develop in culture.

Shaw ('13) has contributed interesting notes on diseases of plants in India attributed to two species of *Rhizoctonia.* Unfortunately, however, he has added to the general confusion regarding this subject by a preliminary discussion which does not sufficiently designate the forms referred to, but more especially by the advancement of certain ideas regarding species which are made, apparently, without adequate study of material from other countries. The conclusions arrived at are necessarily at variance with our present knowledge of the forms of *Rhizoctonia.*

Of the organisms producing diseases in Indian crops he refers to *Rhizoctonia Solani* Kühn, a fungus which he found on jute, mulberry, cotton, groundnut, and cowpea. The mode of branching of young hyphae of his fungus is characteristic of *R. Solani,* but with this the resemblance apparently ceases. Basing an opinion wholly upon his descriptions and figures, the adult mycelium (Shaw, '13, pl. 7 and 8) differs from *R. Solani* (1) in being usually much finer; (2) in the abundant development of short "barrel-shaped" cells in the ordinary

vegetative mycelium, which would seem, from his figures, to have little in common with the chain-like, ovoidal, often branched or lobed cells (designated "barrel-shaped" by Balls) of *R. Solani* (see Atkinson, '92, '95; Balls, '05, '06; Duggar, '99; Duggar and Stewart, '01; and others); and (3) in the verrucose or warty, wall markings (Shaw, '13, pl. 8, figs. 2–3), all of which indicate some other fungus.

Again, the development of sclerotia (Shaw, '13, pl. 8, fig. 4) discloses a type of hyphal cell not characteristic of *R. Solani;* and the small discrete sclerotia themselves (Shaw, '13, pl. 2, fig. 3, pl. 8, fig. 1) convincingly indicate that another fungus was under consideration. I can find no record of a description of sclerotia resembling these in the literature of Rhizoctonia diseases. I am at a loss to understand how a fungus with such characteristics could be likened to Kühn's fungus on the potato, even though depending upon Kühn's imperfect description. On the other hand, neither in general appearance nor in structure (as described and figured by Shaw) am I able to find any resemblance to the "small sclerotia" or infection cushions of *R. Crocorum* (*R. violacea*).

In moist situations the sclerotia of *Rhizoctonia Solani* may occur on aerial organs (as on the pods of beans, Hedgcock, '04, on lettuce leaves, Stone and Smith, '00) but the frequent and apparently normal occurrence of minute sclerotia, fairly regularly arranged, on the dead tips of stems, as described by Shaw, finds no parallel in *R. Solani.* Again, in regard to the hyphae, it may be said that while there is a characteristic location of the septum when a branch is formed in a hypha of *Rhizoctonia,* this character alone is not sufficient to identify the fungus. It is necessary to take into consideration all of the mycelial characteristics which have been referred to, and if possible also the cultural characters. The writer finds that the "Rhizoctonia type" of branching is more or less similar to that found in the hyphae of certain species of *Sclerotinia, Morchella, Pleospora, Rosellinia,* and many others. It would be unwise to offer any definite suggestions regarding the fungus described by Shaw and referred to above. What relation it may bear to the fungus of "bangle blight" (Cunning-

ham, '97) must also remain, for the present, uncertain. It is possible that Shaw's fungus is one of the *Ascomycetes,* at least this is suggested by the figures of the sclerotia.

In my opinion Shaw has correctly referred to *Corticium vagum* B. & C. (accordingly to *Rhizoctonia Solani* Kühn, representing the vegetative phases of that species) another fungus which he also found in India on the groundnut and cowpea. Both the mycelium and the sclerotia of this second organism as described by him agree with *R. Solani* as we know it on carnation, beet, bean, lettuce, potato, etc., in America and elsewhere, as far as reported. The descriptions and measurements of basidia and spores are also in sufficient accord.

Shaw has even suggested that *Rhizoctonia violacea* Tul. is the vegetative stage of *Corticium vagum* B. & C. No such unfortunate confusion could result, however, had he been able to study that which is accepted as Kühn's organism on the potato together with the violet root felt fungus of Europe on any of its hosts. He has obviously failed to find material of the last named fungus in his studies thus far.

Between *Rhizoctonia Crocorum* and *R. Solani* in the vegetative condition some of the important and easily observed contrasting features as usually found are presented in the following table:

Rhizoctonia Crocorum	Rhizoctonia Solani
An external felt, or mantle, of investing hyphae, confined almost exclusively to underground organs.	External mycelium, if noticeable, only a web, or sometimes with flaky tufts, the formation of a "collar" occurring only at the time of fruiting.
Color of mycelial felt pink-red or violet to violet-brown with age.	Color of web, if evident, dirty yellow to yellow-brown.
Protoplasm of young hyphal cells soon develops a violet reddish pigment.	Young hyphal cells hyaline, and even when flavous later, pigment confined to walls.
Infection cushions conspicuous in the root-investing mycelium on most hosts.	Nothing comparable to infection cushions, though on potato sclerotia may serve as points of infection.

Sclerotia, when present, densely wooly with investing mycelium and filaments of short, ovoidal or elliptical hyphal cells. Internal structure not truly plectenchymatic, cells variable in size.	Sclerotia normally free from any definite or permanent investment of mycelium, or filaments of elbowed hyphal cells. Internal structure homogeneous in the larger, denser sclerotia.
Cultures difficult,—not yet obtained by usual methods.	Cultures readily obtained on any nutrient medium.
Typically a parasite, with perhaps the possibility of continuing existence only for a time saprophytically.	Grows rapidly saprophytically on the invaded host, and apparently on debris in the soil when conditions are favorable.

The following species may be excluded from *Rhizoctonia* as far as can be judged from reference to the descriptions and to the exsiccati material examined:

Rhizoctonia Allii Graves, de Thuemen, Myc. Univ. Fasc. 6: *600* (obviously not closely related to the forms here discussed). *R. bicolor* Ell. N. Am. Fung. Fasc. 10: *977* (with sclerotia like those of a Botrytis, e. g., *B. cinerea*). *R. Brassicarum* Lib., Libert, Pl. Crypt. Arduennae, Fasc. 3 : *240* (no characteristics of *Rhizoctonia*). *R. muscorum* Fr. Ellis, N. Am. Fung. Fasc. 13 : *1266;* Libert, Pl. Crypt. Arduennae, Fasc. 2 : *141.*

From the descriptions alone it would seem that the following species have insufficient affinities with *Rhizoctonia* to be included, but critical study of material is needed:

Rhizoctonia aurantiaca Ell. & Ev. on decaying wood of Acer; *R. Batatas* Fr. on *Ipomoea Batatas; R. placenta* Schw., and *R. radiciformis* Schw., on decaying wood (the three last mentioned are distributed in Schweinitz', Syn. N. Am. Fung., to which, however, the writer has not yet had access); *R. destruens* Tassi, reported parasitic on five species of *Delphinium,* and on *Lobelia laxiflora,* and *Hibiscus rosa-sinensis; R. moniliformis* Ell. & Ev. on branches of *Nyssa.*

Rhizoctonia Strobi Scholz ('97) on roots of *Pinus strobus* in Austria, is insufficiently described to warrant a suggestion; and *R. subepigea* Bertoni ('97) on coffee should be included in a further comparative study.

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SOME RELATIONS OF PLANTS TO DISTILLED WATER AND CERTAIN DILUTE TOXIC SOLUTIONS

M. C. MERRILL

Formerly Research Assistant to the Missouri Botanical Garden

I. Introduction

In view of the extensive use of distilled water as a medium in which to grow control plants for comparative purposes in solution-culture work, there is well-grounded justification for the performance of considerable experimental work in order to determine more definitely the relations of plants to this medium. The subject is an important one, and it will require much experimentation for the ultimate solution of all phases of the problem involved. While the results herewith reported are only preliminary in their nature, the fact that they give positive indications along certain lines has been deemed sufficient warrant for their publication at this time. In addition to determining the growth relations of plants in this and other media, consideration has also been given to the effect produced by growing plants in this medium as determined by means of electrical conductivity measurements.

II. Historical Aspects of the Subject

The relation of plants to distilled water is a matter that has been under more or less serious consideration at different periods for a long time. Woodward (1699), who first employed the method of water culture in 1691–1692 in his interesting experiments, found that plants grew better in river water than in either rain water, spring water, or distilled water. The difference was of course due to the quantity of plant food contained in the medium, and this idea, coupled also with the character of the nutrients, has been the basis for a vast amount of physiological work since that time.

Coming down to more modern times, there has been a diversity of opinion among the investigators of the subject

in regard to the reason why plants and animals thrive so much better in natural water or aqueous media than in distilled water. Considering the period from about 1860 on down to the present, the most important explanations offered may be summed up under the following three heads:

1. Lack of essential nutrients;
2. The presence of deleterious substances;
3. Extraction of salts, or nutrient materials, from the organism immersed in the distilled water.

Holding each of these views there has been a formidable array of scientists at different periods, each group contending strongly to establish the correctness of its viewpoint.

Among the earlier workers in the field may be mentioned Boehm ('75), Dehérain ('78), and others, who believed that the lack of essential nutrients in the distilled water was responsible for the resulting poor condition of the organism. Boehm, for example, believed that calcium played a fundamental rôle in the metabolism of the plant, and that in its absence certain processes, notably that of starch formation, could not be carried on and that therefore deterioration resulted. He also believed that calcium was necessary for the transfer of the reserve materials from the cotyledons to the formative organs. Dehérain repeated Boehm's experiments and confirmed his results.

Owing to the fact that even distilled water, which had been unquestioningly regarded as pure, produced effects simulating toxicity, a great deal of attention has been given in the past to the chemical and other properties of water distilled from different kinds of apparatus and under various conditions. On the animal side, workers, among whom may be mentioned Kölliker ('56) and Nasse ('69), had early noticed the injurious effects on tissues when the same were placed in distilled water. Nasse, for example, found the deleterious effect of distilled water about equal to that of the following solutions: 2.5 per cent NaCl, 3.3 per cent NaBr, 3.7 per cent Na_2SO_4, and 5.0 per cent NaI.

Nägeli ('93), in his classical work published twelve years after his death, found that very minute amounts of toxic sub-

stances, notably copper, in solution produced injurious effects on organisms (*Spirogyra*), and to this phenomenon he applied the term "oligodynamik" action. This line of work was extended to include other substances and other organisms, and claimed the attention at different times of Aschoff ('90), Loew ('91), Locke ('95), Ringer ('97), Copeland and Kahlenberg ('99), Dehérain and Demoussy ('01), Lyon ('04), Bokorny ('05), Hoyt ('13), and others. It is of particular interest to note that Ringer in some of his earlier work ascribed the injury to the extraction from the organism of necessary nutrient materials; but after the publication of Locke's experiments ('95), which Ringer duplicated and confirmed, the latter concluded that the injury done in the particular case under consideration (*Tubifex*) was due to deleterious materials in the distilled water. He says: "Copper in even infinitesimal quantities will disintegrate tubifex whilst water free from copper or other heavy metals and without any salts such as calcium salts can sustain the life of tubifex."

In regard to the third idea pertaining to the effects of distilled water on organisms, early workers, both on the plant and animal side, found that salts were extracted from organisms placed in distilled water, even though their methods for determining the extraction were somewhat crude. Among the early investigators on the animal side may be mentioned Plateau ('83), Ringer and his school ('83, '84, '85, '94, '94[a], '94[b], '97), Loeb ('03), and others. The writer has another paper ready for publication in which is given a historical treatment of the subject of excretions from roots and other plant parts, so the discussion of certain phases of the plant work is reserved for that publication.

Upon the perfection and the employment of conductivity apparatus by physical chemists, it soon began to be used also by the various workers in the fields of soil, plant, and animal investigations. In this connection distilled water came in for its share of consideration. The determination of the purity of water by ascertaining its electrical conductivity speedily came into vogue, and it should be said that as far as elec-

trolytes are concerned it is a very accurate and excellent method and has deservedly come into more and more general use for this purpose in the fields of chemistry, physics, and biology.

Koeppe ('98), for instance, determined the electrical conductivity of water obtained from various sources and compared his results with those of other workers. He believed that distilled water has a deleterious effect which is partly due to a withdrawal of salts necessary to the organism, and partly to a swelling of the tissues. He was supported in his views by Oldham ('09), while Winckler ('04), Kobert ('05), and others argued in favor of the harmlessness of distilled water, especially in medical practice. Peters ('04) used the electrolytic conductivity method in his work on *Stentor* and found that there was an exosmosis of electrolytes when the organism was placed in distilled water, and he therefore concluded that the injurious effects noted were due to an extraction of salts. True and Bartlett ('12, '15, '15[a]) considered, for certain salts, not only the excretion but also the absorption of electrolytes under balanced and unbalanced conditions of the medium.

In a recent paper in which a historical discussion of the subject is also given, True ('14) concludes that over and above any injurious effects caused by deleterious substances in the distilled water there is still a "residuum of harmful action due to no known type of impurity." Because this harmful action seems to be most marked in water of least conductivity True believes that the withdrawal of electrolytes from the root tissues best accounts for the deleterious action, but that this withdrawal is "not due to the aggregate difference in osmotic pressure between the cells of the roots and the external medium." He chose lupine seedlings for his work because Frank ('88) had found them very sensitive to distilled water. Schulze ('91), however, after several years of experience with *Lupinus luteus,* claimed that distilled water produced no toxic effects upon those plants.

Both before and after the appearance of the recent contribution by True just referred to, I carried on the investi-

gations reported in this paper, which, as previously stated, are but preliminary in their nature, but which have given indications leading to the conception of an idea differing somewhat from the majority of those above mentioned regarding the relation between plants and distilled water. This conception will be briefly mentioned here, while the evidence and a further discussion will be given later; it is that pure distilled water is not harmful or injurious *per se,* but that because of the static condition forced upon them as a consequence of the absence of plant food, the growing cells become disorganized and thus become easy prey to bacterial and fungous action. Excretion of electrolytes does occur but this should be considered merely as a concomitant condition, or resulting effect of the conditions under which the plants are placed, and should not be considered as a *cause* of degeneration unless the electrolytes themselves be toxic.

III. Methods

(Germination, Culture, and Conductivity)

Canada field peas (*Pisum sativum*) and horse beans (*Vicia faba*), the small variety, were the plants selected, as both were known to be well adapted for growth in solution cultures. Of the various methods of seed sterilization tried out, the one in which the seeds were treated with 1–600 formalin-water for 15 minutes after being soaked for 24 hours in running water gave best satisfaction.

For germinating the seeds a modification of the method used by Boussingault ('74), and also by various investigators in the Bureau of Soils, was employed. This consisted in the use of ordinary enameled-ware pans about 12 inches in diameter and 3 inches in height, filled with tap water and covered with 6 × 6-mesh galvanized iron "hardware cloth," on which the previously soaked and sterilized seeds were placed. The seeds were then covered with filter paper or paper towelling which was kept moist throughout the germination process or until the radicles reached the water below. The germination was carried on in the greenhouse. In the

course of four or five days a splendid lot of vigorous, uniform seedlings which have serviceably straight radicles about 2 inches long with no laterals yet formed is obtained by this method; such seedlings are well adapted, both by their character and their accommodation to an aqueous medium, for solution-culture work. At this stage the plumules have grown to about one-half inch in length, and the plants are now ready for transfer to the culture medium, an operation which is easily and quickly done. This method of germination, which is shown in pl. 16 fig. 2, recommends itself both by reason of its simplicity and ease of operation and the certainty of securing excellent results. In the transfer process from the germinating pan to the culture medium, the entire seedling was always immersed and carefully rinsed in once-distilled and again in twice-distilled water; by this means the roots became free of any adhering impurities.

As containers for the cultures, ordinary glass tumblers were used, the sides of which were covered with black paper to prevent algal growth and the top covered with perforated paraffin paper. (For a complete description and illustration of the method see the paper by McCool, '13.) Ten plants were grown in most cases in each tumbler; exceptions to that number will be noted in each case when the series are discussed in detail. Galvanized iron wire supports were used to hold the plants upright when the seedlings had attained sufficient size to require them.

In all cases doubly distilled water was used, the second distillation being carried out in the laboratory with $KMnO_4$ added to the once-distilled water to oxidize any organic matter that might be present. Conductivity tests of this water showed it to possess a specific conductivity of 2.064×10^{-6}. The nutrient solution used was that of Pfeffer, redistilled water being the solvent for the necessary salts. Each tumbler was filled to a convenient level with either the water or the full nutrient solution as the case might be, approximately 250 cc. being required. To replace transpiration loss, doubly distilled water was added as needed.

In the early days of conductivity work on solutions,

measurements could be made only by means of a continuous current. Because of the resulting polarization effects, however, the resistance of the solution increased to such an extent as to introduce serious errors into the results. But thanks to the classical work of Kohlrausch and others, the alternating current method was devised and perfected, whereby the determinations became practically independent of polarization effects. A vast amount of work has since been done in the realm of physical chemistry on conductivity measurements, a review of which, however, is outside the scope of this paper. For a clear and concise discussion of this subject see Jones ('09), Walker ('10), or Findlay ('10).

In addition to the investigations already cited which deal with the practical applications of conductivity work, there might well be mentioned in this connection the work done by investigators in the Bureau of Soils of the U. S. Department of Agriculture: Whitney, Gardner, and Briggs ('97); Whitney and Briggs ('97); Whitney and Means ('97); and Gardner ('98). Heald ('02) used the Kohlrausch method for determining the conductivity of plant juices in order to get indications regarding the dissolved mineral substances in different parts of the plants under experimentation. Nicolosi-Roncati ('07), Bouyoucos ('12), Dixon and Atkins ('13, '13[a]) and others have also carried on conductivity determinations with different plants and under various conditions.

Sjöqvist ('95) was the first to use the conductivity method in enzyme investigations, which he did in his work on the action of pepsin on protein solutions. Similar work was done by Oker-Blom ('02), who also extended the applications of this method. Oker-Blom ('12) has recently given an account of his own and previous investigations in the field of bacteriology, wherein the electrical conductivity method was used. Various other investigators have also made use of it, among whom may be mentioned Bayliss ('07). Stiles and Jörgensen ('14) give a partial review of some of the historical aspects of this subject as it pertains to plant work.

For the conductivity work herein reported the following apparatus was used:

Wheatstone bridge (Central Scientific Co., catalogue number, 2475);
Resistance box, 11,110 ohms (Central Scientific Co., catalogue number, 2444);
Induction coil (Eimer and Amend, catalogue number, 4100);
Dry battery cells (Eimer and Amend, catalogue number, 592);
Conductivity cell, Freas (Eimer and Amend, catalogue number, 5202);
Telephone receiver (Central Scientific Co., catalogue number, 2355);
Thermometer graduated to 1/10°C;
Water tank holding 50 gallons, specially constructed for the purpose, pilot flame underneath; temperature regulated to 1/10°C;
Tiffany laboratory motor with which to operate a stirring apparatus in the tank.

In the method employed for the work the procedure given below was consistently followed: the tumblers were always filled to approximately the 250 cc. level with either the solution or redistilled water, depending on the culture. Before taking readings, doubly distilled water was added to bring the water or solution up to the original level, if the transpiration loss since the previous reading made the addition necessary. This was of course essential in order to keep the concentration factor under control. Readings in all cases were taken at 25°C. The control of temperature exactly to within 1/10°C. was comparatively easy by the use of the pilot flame underneath and the stirring apparatus in the tank of water.

For absolutely accurate and final quantitative determinations or ultimate values, as were required, for example, in the case of the standardization measurements for the cell constant with N/50 KCl, or the determination of the specific conductivity of the doubly distilled water, the greatest precautions possible were taken in regard to the conductivity cell and the concentration of its contents. But in making hundreds and even thousands of determinations, most of them as rapidly as accuracy permitted, due to the time factor involved, it was both impossible and unnecessary to dry the cell after each reading, since relative, and not absolute, values were

desired for the most part. The method employed, therefore, was to remove from the carefully stirred solution in the tumbler a 25 cc. sample with a pipette of the same capacity, the latter having previously been rinsed with the solution. Using exactly the same amount for each determination further reduced any possibility of error due to unequal dilution in the conductivity cell. Between readings the pipette was kept almost entirely immersed in redistilled water in a tall cylinder attached to a stand in the water bath. After carefully pouring the sample back into the tumbler, in case further readings were to be taken, the cell was rinsed twice with doubly distilled water and rapidly drained before taking the next reading, whether of the same or of a different culture. Any minute amount of doubly distilled water that might be present to dilute the next sample was a constant factor throughout all the readings and was of course inconsequential.

In using fresh batteries it was necessary to insert resistance coils between the battery and the induction coil in order to reduce the current. For this purpose German silver wire was used. While polarization phenomena may possibly be operative to a certain extent, such would be so small as to be practically negligible, especially in view of the fact that the effects from such a cause would be entirely relative and would therefore not affect the validity of the results.

Some of the conductivity results given in this paper are shown in tabular form and others are plotted as curves. In some instances the data are calculated as specific conductivity; in other cases the conductivity is represented by the value of x on the Wheatstone bridge. To make it clear what x actually represents, when the apparatus is set up as it was for the determinations, the following proportion is given:

$$R : R' :: x : 100—x$$

R is the resistance in ohms inserted in the resistance box; R′ is the resistance in ohms of the solution; and x is the number on the bridge wire (graduated in millimeters from 0 to 100 centimeters). As the position of x on the bridge varies with R and R′, the R for each series of curves or tables will be given (though in the great majority of cases it was 9,110),

from which R′ can then be calculated. Having these values, the specific conductivity can be calculated for any determined cell constant (the value of the cell used being .4088). For a fuller discussion see Findlay ('10).

IV. Recovery of Plants after being in Distilled Water for Varying Periods

The first question studied pertained to the recovery of plants in full nutrient solution after being kept in doubly distilled water for varying periods. To determine the comparative condition for optimum recovery, the distilled water and the full nutrient medium were renewed every four days in some cultures and left unrenewed in others, in such a way that for either condition of the medium of each set in a certain period the other medium would be both renewed and unrenewed so as to give all possible methods of combination. Examination of table 1 will make this clear. Thus, for example, with cultures 11, 12, 13, and 14 of the 10-day period in distilled water the doubly distilled water in Nos. 11 and 12 was unrenewed; but when these cultures were placed in full nutrient solution this medium was unchanged or unrenewed for No. 11 and was renewed for No. 12. The distilled water in Nos. 13 and 14 was renewed, and the full nutrient solution unrenewed and renewed respectively.

In series 1 the small variety of horse beans (*Vicia faba*) was employed, 8 plants being used to a culture. The condition of the media and duration of growth, the green weight of tops, and the dry weight of tops and roots of series 1 are given in table 1. On examining this table it is seen that even after the plants had remained for 20 days in distilled water, they recovered on being placed in the full nutrient solution, while those remaining for 10 days in distilled water produced practically as much growth when later placed in the full nutrient solution as did the plants which were in the latter medium during the entire period.

Of course, as would be expected, the cultures wherein the full nutrient solution was renewed every four days gave much better growth than did those in the unrenewed medium, due,

no doubt, to an increased amount of available nutrients. But an interesting comparison is manifest in connection with the effect of renewing the distilled water; the greater growth of both tops and roots may be noted in cultures 3 and 4, in which

TABLE I (Series 1)

EFFECT OF RENEWED VS. UNRENEWED MEDIA ON GROWTH OF HORSE BEANS

Culture no.	Length of period in dist. H_2O days	Dist. H_2O renewed or unrenewed	Length of period in full nutr. days	Full nutr. renewed or unrenewed	Green wt. of tops gms.	Dry wt. of tops gms.	Dry wt. of roots gms.
1	45	Unrenewed	.....	.....	2.15	.777	.124
2	45	Unrenewed	.....	.....	1.75	.666	.096
3	45	Renewed	.....	.....	4.40	.887	.272
4	45	Renewed	.....	.....	4.40	.870	.235
5	1	Unrenewed	44	Unrenewed	16.30	2.069	.485
6	1	Unrenewed	44	Renewed	27.00	3.069	.707
7	2	Unrenewed	43	Unrenewed	15.85	1.994	.429
8	2	Unrenewed	43	Renewed	32.51	3.543	.743
9	5	Unrenewed	40	Unrenewed	18.90	2.315	.463
10	5	Unrenewed	40	Renewed	26.25	2.895	.700
11	10	Unrenewed	35	Unrenewed	13.35	1.623	.382
12	10	Unrenewed	35	Renewed	26.35	2.928	.697
13	10	Renewed	35	Unrenewed	14.90	1.887	.463
14	10	Renewed	35	Renewed	22.90	2.376	.548
15	15	Unrenewed	30	Unrenewed	14.00	1.719	.388
16	15	Unrenewed	30	Renewed	18.05	1.880	.457
17	15	Renewed	30	Unrenewed	15.60	1.807	.417
18	15	Renewed	30	Renewed	21.20	2.403	.642
19	20	Unrenewed	25	Unrenewed	12.51	1.447	.300
20	20	Unrenewed	25	Renewed	11.40	1.247	.328
21	20	Renewed	25	Unrenewed	11.40	1.319	.284
22	20	Renewed	25	Renewed	15.50	1.670	.454
23	.....	.....	45	Unrenewed	14.60	1.975	.419
24	.....	.....	45	Unrenewed	14.70	2.044	.443
25	.....	.....	45	Renewed	27.85	2.925	.690
26	.....	.....	45	Renewed	27.05	3.025	.764

the distilled water was renewed every four days throughout the period, as compared with that of cultures 1 and 2, where the distilled water was not renewed, except, of course, for the occasional addition of water to replace the transpiration loss, which, however, was small. Furthermore, in noting the growth of cultures 11–22 inclusive, it is seen that in four of the six cases of comparison between the renewed and unrenewed distilled water, better growth of both tops and roots resulted where the distilled water was renewed. Considering cultures 1–4 and 11–22, inclusive, the total green weight of tops for the unrenewed distilled water as compared with the

renewed distilled water, and the same conditions for the dry weight of tops and roots, gave the results to be seen in table II. The total weight in all cases is therefore greater in the cultures in which the distilled water was renewed.

TABLE II (Series 1)
EFFECT OF RENEWED VS. UNRENEWED DISTILLED WATER ON GROWTH OF HORSE BEANS
(Summarized Results of Part of Table I)

Medium	Green wt. of tops in grams	Dry wt. of tops in grams	Dry wt. of roots in grams
Water renewed...	110.30	13.219	3.315
Water unrenewed	99.56	12.287	2.772

These results therefore indicate that the so-called injury to plants in distilled water cannot be entirely or even satisfactorily explained on the basis of extraction of solutes from the plant tissues. If that were the case we should have the greatest injury and least recovery in those cultures in which the distilled water was renewed, the periodically renewed water effecting *in toto* a greater exosmosis of the salts than the water which is not renewed. This statement will receive verification under the section on conductivity measurements. It would therefore seem that we must seek other explanations for the phenomena observed when plants are placed in distilled water. This phase of the subject will also be discussed later.

The points noted will be clear from an examination of pl. 13 figs. 1 and 2. Plate 13 fig. 1 shows the various stages of recovery after varying periods in the distilled water. The better growth is to be noted of both tops and roots of No. 2, in which the distilled water was renewed, as contrasted with No. 1, in which it was not renewed. It is interesting to observe how plants, even after 20 days in distilled water, will recover in full nutrient solution and then give even better growth than plants in unrenewed full nutrient solution the entire period, and that after 10 days in distilled water, plants will recover in renewed full nutrient solution and equal in

growth, plants grown the entire period in renewed full nutrient solution.

Plate 13 fig. 2 shows first (Nos. 1 and 2) the contrasted effect of renewing and not renewing the full nutrient solution. The remaining 8 cultures of the plate show the effect of renewing and of not renewing both the distilled water and the full nutrient solution. In cultures 3–10 the comparison should, of course, be made between the alternating numbers for the distilled water effect (renewed or not renewed), and between successive numbers for the effect of the renewal or the non-renewal of the full nutrient solution. While the culture represented by No. 7 of the plate gave greater growth than did No. 9, that excess was probably due to the individual hardihood of two plants. It is seen that a much more uniform and desirable growth was made by the plants of No. 9.

An interesting point in connection with the horse beans is that 16 days after setting up the series the tips of those plants still in distilled water were more or less blackened, probably as a result of enzyme (oxydase) action, and many of them were considerably inrolled. Such conditions were entirely absent from the cultures in full nutrient solution at that time. When the affected plants were later placed in full nutrient solution there was a gradual recovery from the blackening of the leaves, and this recovery was greater in the case of those cultures in which the distilled water had been renewed than in those in which it had not been renewed. Twenty days later Nos. 3 and 4 were in very much better condition than Nos. 1 and 2. There was much less blackening, some leaves not being blackened at all. The general height of the plants in Nos. 1 and 2 was $1\frac{1}{2}$–$2\frac{1}{2}$ inches; and in Nos. 3 and 4 it was $2\frac{1}{2}$–4 inches. A very noticeable feature at the end of the experiment was the condition of the medium, that of Nos. 3 and 4 being of course clear while that of Nos. 1 and 2 was milky, turbid, and opaque, indicating abundant fungous and bacterial action, a condition further emphasized by the hyphal threads and gelatinous coating on the roots.

The roots of the plants in Nos. 3 and 4 were also in much better condition at the end of the experiment than were those

of Nos. 1 and 2, especially as regards length and the amount of lateral root development. The root growth in No. 13 at the end of the experiment was also greater than that in No. 11; but in Nos. 12 and 14 it was about equal. The plants of No. 17 also showed greater root growth than did those of No. 15, and this difference was more marked than in the case of the tops. The lateral roots in No. 17 were produced all along the main roots, while in No. 15 they were practically confined to the upper or older portion of the main roots. Another interesting difference observed was that in No. 17 the main root tips were not permanently injured in the distilled water and when placed in the full nutrient solution they continued growth. This was not the case in No. 15. In general there was not much difference between the roots in Nos. 16 and 18; the plants in No. 18, however, had slightly greater growth of roots and showed less injury and some continuation of growth of the tips, whereas those in No. 16 did not. The same condition of the roots above noted for Nos. 15 and 17 held also in Nos. 19 and 21 respectively; but the difference in favor of the renewal of the distilled water though less marked was nevertheless evident. Likewise, Nos. 18 and 20 were similar to Nos. 16 and 18 respectively.

Strong evidence was therefore afforded by the cultures of horse beans that renewing the distilled water has a favorable effect upon the plants.

Series 2 is in every respect a duplicate of series 1 except that Canada field peas (*Pisum sativum*) were used instead of horse beans (*Vicia faba*), and that the dry weight of the tops was not determined; furthermore, the length of the experimental period was different. The condition of the media and duration of growth, the green weight of tops, and the dry weight of roots are given in table III, seven plants being grown in each culture. An examination of this table reveals results similar in many cases to those contained in table I; plants recovered even after 20 days in distilled water, but after 10 days in this medium the recovery was not so complete as in the case of the horse beans, for the plants so treated did not equal in growth similar ones which had remained in

full nutrient solution the entire period. However, plants which had been in distilled water only 5 days before being transferred to full nutrient solution subsequently equalled in growth other plants which had been in the latter medium from

TABLE III (Series 2)

EFFECT OF RENEWED VS. UNRENEWED MEDIA ON GROWTH OF PEAS

Culture no.	Length of period in dist. H_2O days	Dist. H_2O renewed or unrenewed	Length of period in full nutr. days	Full nutr. renewed or unrenewed	Green wt. of tops gms.	Dry wt. of roots gms.
1	47	Unrenewed	.....	.....	.80	.073
2	47	Unrenewed	.....	.....	.60	.076
3	47	Renewed	.....	.....	.45	.067
4	47	Renewed	.....	.....	1.30	.091
5	1	Unrenewed	32	Unrenewed	6.75	.400
6	1	Unrenewed	32	Renewed	11.05	.500
7	2	Unrenewed	31	Unrenewed	5.50	.401
8	2	Unrenewed	31	Renewed	12.90	.568
9	5	Unrenewed	28	Unrenewed	5.95	.263
10	5	Unrenewed	28	Renewed	12.35	.467
11	10	Unrenewed	23	Unrenewed	5.35	.254
12	10	Unrenewed	23	Renewed	7.90	.321
13	10	Renewed	23	Unrenewed	3.80	.160
14	10	Renewed	23	Renewed	6.07	.202
15	15	Unrenewed	18	Unrenewed	3.30	.144
16	15	Unrenewed	18	Renewed	4.40	.175
17	15	Renewed	18	Unrenewed	4.30	.162
18	15	Renewed	18	Renewed	4.15	.169
19	20	Unrenewed	13	Unrenewed	3.21	.124
20	20	Unrenewed	13	Renewed	2.52	.092
21	20	Renewed	13	Unrenewed	4.05	.139
22	20	Renewed	13	Renewed	4.43	.141
23	.....	.....	33	Unrenewed	5.50	.368
24	.....	.....	33	Unrenewed	6.94	.420
25	.....	.....	33	Renewed	9.60	.536
26	.....	.....	33	Renewed	13.45	.611

the start. The period between 5 and 10 days in distilled water is therefore a critical one, and will be discussed later in other connections.

Renewing the full nutrient solution again showed beneficial results, as might be expected. But the renewal of the distilled water did not produce such striking results in some respects as in the case of the horse beans; in other ways, however, the results were equally or even more striking. Where the plants remained in distilled water for 47 days the growth was better in one case and poorer in the other where the distilled water was renewed than where it was not renewed. The average

growth, however, of the two cultures in the renewed medium was better than that of the two in the unrenewed distilled water.

In Nos. 11–22, there was better growth of tops and roots

TABLE IV (Series 2)

EFFECT OF RENEWED VS. UNRENEWED DISTILLED WATER ON GROWTH OF PEAS
(Summarized Results of Part of Table III)

Medium	Green wt. of tops in grams	Dry wt. of roots in grams
Distilled water renewed...	28.55	1.131
Distilled water unrenewed.	28.08	1.259

in four cases where the distilled water was renewed and better growth in four cases where it was not renewed. Considering cultures 1–4 and 11–22 the results given in table IV were obtained, from which it is again evident that renewing the distilled water exercises no injurious influence, and the conclusion is reinforced that an exosmosis of mineral nutrients is not the fundamental basis of the injury which plants suffer in distilled water. Furthermore, the difference between the renewed and the unrenewed distilled water cultures was very marked if the plants remained for 20 days in distilled water before being changed to the full nutrient solution, the difference being greatly in favor of the cultures in which the medium was renewed.

Figures 1 and 2 of pl. 14 illustrate the points above mentioned. In pl. 14 fig. 2 should be noted the better growth of Nos. 9 and 10—which were in renewed distilled water for 20 days before transfer to full nutrient solution—as compared with Nos. 7 and 8, which had remained in unrenewed distilled water for the same length of time before transfer. The excess of growth in No. 4 over that in No. 6 is probably to be accounted for on the ground that since those cultures were in distilled water but 10 days neither the renewal nor the unrenewal of the medium exercised much effect. Hence the greater growth of No. 4 represents an individual variation.

At the expiration of the experimental period the following conditions prevailed in series 2: while the top growth in

cultures 1–4 was about the same in each case, the root growth in Nos. 3 and 4 was much better than that in Nos. 1 and 2, the roots of the former being whiter, cleaner, and having longer and more numerous lateral roots. In the case of those cultures grown in distilled water 10 days before removal to full nutrient solution, Nos. 11 and 12 were in somewhat better condition than Nos. 13 and 14, a difference which might readily be expected for the shorter periods in distilled water due to individual variation. After 15 days in distilled water and 18 days in full nutrient solution the benefits derived from renewing the former were markedly evident in the appearance of cultures 15–18, even though the actual weights did not show such difference. Nos. 17 and 18 were in better condition than Nos. 15 and 16 respectively, especially as regards the root growth; similarly, Nos. 21 and 22 were in better condition than Nos. 19 and 20 respectively.

Some special conditions which are of particular interest were observed when the cultures were examined carefully at the close of the experiment. The first point pertains to the method of recovery. After being in the distilled water only one or two days the top growth of such cultures when placed in full nutrient solution proceeds unhindered from the tips of the main stems, i. e., the tips of the stems remain uninjured and resume growth. But 5 days in distilled water almost marks the limit at which growth can be resumed at the tip of the main axis of the stem when such cultures are subsequently placed in full nutrient solution. After 10 days in distilled water the tips of the stems become injured so that the later growth in full nutrient solution is made from new lateral branches. Hence the period from 5 to 10 days in distilled water before removal to full nutrient solution may be considered a crucial period as regards the recovery and growth of the main stems.

Another point of interest is the delayed maturity which results in the case of the cultures which are grown for some time in distilled water and later are placed in full nutrient solution. Such plants remain in a green and growing condition much longer than do those which have been in full

nutrient solution for the entire period, or those which remained in distilled water for a shorter period before being transferred to the full nutrient solution. The growing season of the former is thus prolonged and the date of maturity delayed.

The foregoing series having given evidence of the recovery of plants in full nutrient solution after being in distilled water for 20 days, the question arose as to the maximum length of time plants might remain in distilled water without preventing recovery when subsequently transferred to full nutrient solution. Series 3 was therefore set up. This consisted of cultures of Canada field peas grown in distilled water for 10, 20, 30, 40, and 50-day periods before transfer to the full nutrient medium. The condition of the media and duration in each and also the results of the series (as shown by the green weight of tops) are given in table v, Nos. 1–20 inclusive. Renewals in this series also were made every four days. Nos. 21–28 under different conditions and concentration of nutrient solution are given for purposes of comparison. The maximum time limit in distilled water above referred to is thus seen to be approximately 30 days, and this was practically attained only in case of the cultures in renewed distilled water. After 40 days in distilled water, whether renewed or unrenewed, the recovery was almost nil, though somewhat better in the renewed, while after 50 days in either renewed or unrenewed distilled water all the cultures were dead.

In the 10 cases furnishing comparisons between cultures in which the full nutrient solution was preceded on the one hand by renewed and on the other by unrenewed distilled water, greater growth was attained in 7 cases where the distilled water was renewed. The total weight of green tops is more nearly equal in the two sets of cultures, however, being 24.20 grams in the case of those in the unrenewed and 22.38 grams in the case of those in the renewed distilled water. We thus see that no injurious effects attend the renewal of the distilled water when compared with the non-renewal of the same; on the other hand, positive benefits are derived from such a

renewal, especially in the case of plants approaching the maximum time limit of durability in distilled water—a period which enables the results of the two conditions to be more readily seen and compared.

TABLE V (Series 3)

GROWTH OF PEAS IN RENEWED AND UNRENEWED MEDIA FOR VARIOUS PERIODS UP TO THE MAXIMUM TIME FOR SURVIVAL. ALSO EFFECT OF ADDING WATER AT DIFFERENT INTERVALS TO MEDIA UNDER VARIOUS CONDITIONS

Culture no.	Length of period in dist. H_2O days	Dist. H_2O renewed or unrenewed	Length of period in full nutr. days	Full nutr. renewed or unrenewed	Green wt. of tops gms.
1	10	Unrenewed	42	Unrenewed	4.50
2	10	Unrenewed	42	Renewed	8.00
3	10	Renewed	42	Unrenewed	4.85
4	10	Renewed	42	Renewed	6.30
5	20	Unrenewed	32	Unrenewed	2.70
6	20	Unrenewed	32	Renewed	5.05
7	20	Renewed	32	Unrenewed	3.55
8	20	Renewed	32	Renewed	1.40
9	30	Unrenewed	22	Unrenewed	.55
10	30	Unrenewed	22	Renewed	1.30
11	30	Renewed	22	Unrenewed	1.90
12	30	Renewed	22	Renewed	1.90
13	40	Unrenewed	12	Unrenewed	.50
14	40	Unrenewed	12	Renewed	.55
15	40	Renewed	12	Unrenewed	.65
16	40	Renewed	12	Renewed	.72
17	52	Unrenewed	.....	.....	.60
18	52	Unrenewed	.....	.....	.45
19	52	Renewed	.....	.....	.56
20	52	Renewed	.....	.....	.55
21	Unrenewed full nutr. 42 days, dist. H_2O added every 8 days				6.40
22	Unrenewed full nutr. 42 days, dist. H_2O added every 4 days				6.00
23	Renewed full nutr. 42 days, the sol'n. renewed every 8 days				8.75
24	Renewed full nutr. 42 days, the sol'n. renewed every 4 days				18.50
25	Unrenewed 1/10 full nutr. 42 days, dist. H_2O added every 4 d'ys				2.90
26	Unrenewed 1/5 full nutr. 42 days, dist. H_2O added every 8 days				2.95
27	Renewed 1/10 full nutr. 42 days, sol'n. renewed every 4 days				10.10
28	Renewed 1/5 full nutr. 42 days, sol'n. renewed every 8 days				7.85

In pl. 15 fig. 1 some of the cultures are illustrated, the ones of special interest being Nos. 9–14. The exceptionally small or irregular growth of No. 8 is difficult to account for, because in the renewed full nutrient it should be greater than that of No. 7. Individual resistance is apparent, however.

V. Recovery of Plants after being in Toxic Solutions

Having thus ascertained the maximum time plants may remain in distilled water and then recover on being placed in full nutrient solution, we may turn our attention to toxic solutions. If distilled water in itself is toxic then it should be interesting to get quantitative data on its effects as measured by the power of plants so treated to recover. This power should furnish a good index regarding the extent of any injury suffered. By comparing the ultimate time limits for various media after which recovery in full nutrient solution is possible, we are able to get a basis on which to determine the relative toxicity of each medium. Almost simultaneously with series 3, series 4 was set up. The plan of the series and the green weight of tops and dry weight of roots of the plants in series 4 are given in table VI, while pl. 15 fig. 2 shows the actual condition of the plants in some of the media. The results obtained indicate the following relative toxicities of the substances used, the time expressed in days having reference to the longest period in the toxic solution after which recovery is possible:

Redistilled water	30–40 days
N/100 $MgCl_2$	4–8 days
N/1000 $MgCl_2$	about 20 days
N/1000 $CaCl_2$ & N/20 $MgCl_2$	about 16 days
N/12800 H_2SO_4	about 20 days
N/400 KOH	about 20 days

We thus see that as compared with the toxic solutions mentioned distilled water, if it be considered as a toxic agent at all, is much less so than either of the others given above. In this connection it is interesting to note that Kahlenberg and True ('96) found that N/12800 H_2SO_4 and N/400 KOH were approximately the critical concentrations for Lupinus roots. Hence, the fact that plants can remain much longer in distilled water than in these solutions and still recover would seem to indicate that as regards toxicity distilled water is only very slightly if at all deleterious. But the writer believes that it is entirely incorrect and misleading to speak of distilled water as being toxic. What is illustrated above for distilled water is not toxicity, therefore, but merely the length of time

TABLE VI (Series 4)

EFFECT ON GROWTH OF PLANTS OF VARIOUS PERIODS IN TOXIC SOLUTIONS

Culture no.	First sol'n. or medium	Length of period in first medium days	First medium renewed or unrenewed	Length of period in full nutr. days	Green wt. of tops gms.	Dry wt. of roots gms.
1	Dist. H_2O	32	Unrenewed	.....	1.15	.116
2	Dist. H_2O	32	Renewed	.....	1.55	.130
3	N/100 $MgCl_2$	32	Unrenewed	.....	.35	.012
4	N/100 $MgCl_2$	32	Renewed	.....	.40	.016
5	N/100 $MgCl_2$	1	Unrenewed	31	10.15	.428
6	N/100 $MgCl_2$	2	Unrenewed	30	8.40	.372
7	N/100 $MgCl_2$	4	Unrenewed	28	5.15	.132
8	N/100 $MgCl_2$	8	Unrenewed	24	.35	.018
9	N/100 $MgCl_2$	12	Unrenewed	20	.30	.020
10	N/100 $MgCl_2$	16	Unrenewed	16	.40	.016
11	N/100 $MgCl_2$	20	Unrenewed	12	.28	.012
12	N/1000 $MgCl_2$	32	Unrenewed	.....	1.00	.085
13	N/1000 $MgCl_2$	32	Renewed	.....	1.00	.038
14	N/1000 $MgCl_2$	2	Unrenewed	30	8.85	.385
15	N/1000 $MgCl_2$	4	Unrenewed	28	9.70	.384
16	N/1000 $MgCl_2$	8	Unrenewed	24	7.20	.305
17	N/1000 $MgCl_2$	12	Unrenewed	20	5.15	.192
18	N/1000 $MgCl_2$	16	Unrenewed	16	2.05	.121
19	N/1000 $MgCl_2$	20	Unrenewed	12	1.05	.093
20	N/1000 $CaCl_2$ and N/20 $MgCl_2$	32	Unrenewed	.....	.75	.092
21	N/1000 $CaCl_2$ and N/20 $MgCl_2$	32	Renewed	.....	.85	.099
22	N/1000 $CaCl_2$ and N/20 $MgCl_2$	1	Unrenewed	31	10.60	.409
23	N/1000 $CaCl_2$ and N/20 $MgCl_2$	2	Unrenewed	30	9.35	.388
24	N/1000 $CaCl_2$ and N/20 $MgCl_2$	4	Unrenewed	28	10.35	.384
25	N/1000 $CaCl_2$ and N/20 $MgCl_2$	8	Unrenewed	24	8.40	.294
26	N/1000 $CaCl_2$ and N/20 $MgCl_2$	12	Unrenewed	20	3.00	.144
27	N/1000 $CaCl_2$ and N/20 $MgCl_2$	16	Unrenewed	16	1.50	.117
28	N/1000 $CaCl_2$ and N/20 $MgCl_2$	20	Unrenewed	12	.75	.103
29	Full nutr. sol'n.	32	Unrenewed	32	8.95	.411
30	Full nutr. sol'n.	32	Renewed	32	18.50	.530
31	N/12800 H_2SO_4	32	Unrenewed	.....	1.55	.130
32	N/12800 H_2SO_4	32	Renewed	.....	1.25	.124
33	N/12800 H_2SO_4	2	Unrenewed	30	7.05	.318
34	N/12800 H_2SO_4	8	Unrenewed	24	7.45	.289
35	N/12800 H_2SO_4	16	Unrenewed	16	4.40	.236
36	N/12800 H_2SO_4	20	Unrenewed	12	1.95	.172
37	N/400 KOH	32	Unrenewed	.....	1.25	.094
38	N/400 KOH	32	Renewed	.....	1.50	.108
39	N/400 KOH	2	Unrenewed	30	8.60	.444
40	N/400 KOH	8	Unrenewed	24	6.60	.214
41	N/400 KOH	16	Unrenewed	16	2.55	.092
42	N/400 KOH	20	Unrenewed	12	2.60	.117

plants can survive in a medium without nutrient materials. That these plants could not survive for that length of time in the other media, however, shows that in those cases a real toxicity enters into consideration.

In addition to the actual time limits for recovery just tabulated, as well as the method of recovery and delayed maturity mentioned in the preceding section, another interesting point, which was very noticeable in the cultures and which can also be seen in the plates, is the character of growth of the rootlets in the boundary cultures, by which is meant those cultures which have remained in the inimical media nearly as long as their endurance would permit, and whose recovery in full nutrient solution is slower or more difficult than the normal unaffected plants. In the latter case the roots are short and compact and usually extend down only to about one-half the distance to the bottom of the tumbler. In the case of the first mentioned cultures, however, when transferred to full nutrient solution the rootlets develop a long, slender growth easily extending to the bottom of the tumbler.

VI. Effect of Sterilizing the Water During Growth of Plants

The foregoing series pointed, therefore, to factors other than extraction or loss of solute from the plant tissue as being responsible for the deteriorating phenomenon observed when growing plants are placed in distilled water. In the unrenewed water cultures in the previous series a brownish coloration developed and the roots appeared, in their gelatinized condition, to be covered by bacterial and fungous growths. Suspecting that these organisms played an important rôle, it was decided to grow additional cultures to test this point. Four cultures, each containing ten plants of *Pisum sativum*, were set up in distilled water: in one the medium was not renewed; in a second the water was renewed every four days; and in the remaining two the medium was sterilized every four days by boiling in a return condenser one-half hour. The results are given in table VII (series 5) and the cultures are shown in pl. 16 fig. 1. The full nutrient solution cultures

were grown for purposes of comparison. The duration of growth was 30 days.

Whether the beneficial effect of the sterilization was due to the destruction of the bacterial and fungous floras of the

TABLE VII (Series 5)

EFFECT PRODUCED ON GROWTH OF PLANTS BY STERILIZING THE WATER IN WHICH THEY ARE GROWN

Culture no.	Medium	Condition of medium	Green wt. of tops gms.	Dry wt. of roots gms.
1	Dist. H_2O	Unrenewed	1.55	.141
2	Dist. H_2O	Renewed	1.65	.150
3	Dist. H_2O	Sterilized	2.40	.225
4	Dist. H_2O	Sterilized	3.05	.233
5	Full nutr.	Unrenewed	10.30	.342
6	Full nutr.	Renewed	17.65	.507

medium, to a decomposition of any contained toxic substances (thereby rendering them less toxic), or to incidental effects such as aëration of the water by the boiling process, was not definitely determined. Neither was this effect compared with that produced by the addition of various bodies (tannic acid, pyrogallol, calcium carbonate, various hydrates, carbon black, and other substances mentioned by Livingston and his co-workers, '05, '07, Dachnowski, '08, '09, and others). In the last paper of Livingston and his co-workers referred to are given the results of boiling the aqueous extracts from soils containing toxic properties as determined by the growth of plants in the same. The boiling improved the extracts, but this effect was explained by "supposing the process of boiling to remove or change the toxic action of this extract, the toxic materials being perhaps partly volatile with steam." But since in our sterilization process a return condenser was used the removal of toxic substances by volatilization would not occur. A breaking down of toxic compounds into less toxic constituents may possibly be a condition induced by the boiling, however. It will be recalled that Lyon ('04) found the toxicity of tap water reduced by boiling.

While the oxidizing power of roots, due to enzymatic activity, may be an important factor in aiding in the decom-

position of vegetable matter in the soil, as pointed out by Schreiner and Reed ('07) and others, it is not believed that in the case under consideration the oxidizing power of the roots was altered to any appreciable degree by the boiling of the medium. Dachnowski ('12) mentions the effect of oxidation upon the toxic substances found in bog water. In the sterilization method by boiling under a return condenser, however, the aëration or oxidation phenomenon would no doubt play only a subsidiary rôle. The stronger line of evidence seems to favor the destruction of injurious bacterial and fungous agencies as the chief factor in the beneficial effect of the sterilization.

VII. Conductivity Measurements

The excellence of the electrical conductivity method for determining any change in the electrolyte content of an aqueous medium naturally led to its adoption for the experimental work described below. This phase of the investigation was especially concerned with determinations pertaining to the extraction of electrolytes — including the essential nutrient salts—from the roots of plants in distilled water. The generally beneficial results attendant upon a frequent renewal of the distilled water in which the plants were placed has already been noted, as well as the evidence in favor of the view that conditions other than extraction of essential salts constitute the underlying cause of the deterioration of plants in distilled water.

The next point to be determined was the relative amount of the total exosmosis in the renewed distilled water as compared with that in the unrenewed. In placing roots in distilled water it is pertinent to this subject to inquire whether all the exosmosis occurs during the first four days. If it does, we should have the same amount of extraction in both the unrenewed water and that renewed every four days. Or is there a renewal of the exosmosis of the electrolytes following the renewal of the water each time, thereby giving rise to a greater exosmosis than in the cultures in which the water was not renewed? If such a condition obtains and yet in

spite of it the renewal of the water shows no baneful effects, or indeed produces beneficial results, then may we well conclude, and with increasing assurance, that extraction of nutrient salts is in no way responsible for any injury plants undergo in distilled water. The results obtained strongly substantiate that conclusion.

A series of cultures (series 6) was set up in which healthy plants of Canada field peas were grown in full nutrient solution for about three weeks and then transferred, after carefully rinsing the roots, to doubly distilled water. In half of the cultures the distilled water was renewed at certain definite intervals for each culture, while in the other half of the cultures the water was not renewed. Conductivity determinations were then made of the water under both conditions—renewal and non-renewal—at certain regular intervals, varying for each set of cultures, for several days after the plants had been placed in this medium.

By numerous readings it was ascertained that with a resistance of 9,110 ohms in the resistance box the average value of x on the Wheatstone bridge for the water in the vessel after being rinsed and before placing the roots therein was approximately 6.0, rarely varying 1 cm. either way. Considering that figure, then, as the basis or the starting point for the exosmosis, and subtracting it from the different values found for the renewed, and from only the final value obtained for the unrenewed distilled water, we get the figures in the last column of table VIII.

The plan of the experiment with respect to renewal of the distilled water and the time of readings, the values of the individual readings, and the comparative amounts which represent the total exosmosis of the electrolytes under the various conditions of the experiment are all given in table VIII. The numbers given are the values of x on the Wheatstone bridge when the resistance inserted in the box was 9,110 ohms.

It is thus seen that by far the greater exosmosis was obtained in the case of those cultures in which the distilled water was renewed. Another point of interest was the reabsorp-

tion of electrolytes—as seen by the decrease in conductivity of the medium—in those cultures in which the distilled water was not renewed. The reabsorption of electrolytes has been observed to be a phenomenon characteristic of normal, healthy

TABLE VIII (Series 6)
COMPARATIVE EXOSMOSIS IN RENEWED AND UNRENEWED DISTILLED WATER

Culture no.	Water renewal	Conductivity Readings							Duration of treatment days	Total increase in conductivity
		Frequency	1st	2nd	3rd	4th	5th	6th	7th	
1	Every day	Every day	32.9	10.4	10.0	8.9	9.7	9.4	10.2	7	49.5
2	None	Every day	36.3	22.8	21.4	17.8	15.2	12.5	11.4	7	5.4
3	Every 2 days	Every 2 days	10.8	9.3	9.6	10.7	....	....	....	8	16.4
4	None	Every 2 days	25.0	14.3	13.6	11.0	....	....	....	8	5.0
5	Every 4 days	Every 4 days	12.9	15.0	16.1	16.1	....	....	....	16	36.1
6	None	Every 4 days	10.7	12.4	15.9	19.5	....	....	....	16	13.5

peas, when transferred from a full nutrient solution to distilled water, after being in the latter medium one or two days.

In order to obtain some additional information regarding the relations between the conductivity of the medium and the plants grown therein, series 7 containing 50 cultures was set up in full nutrient solution, ten Canada field pea plants to each culture. The nutrient solution was not renewed. At the end of each five-day period 5 of the cultures were taken down, the green weight of tops of the plants in each determined, and the conductivity of the solution measured; and from these results the average green weight of tops and the average conductivity of each set of 5 cultures were obtained. This was done throughout the entire period of 50 days. The results obtained are given in table IX and plotted as curves in fig. 1. In the latter the abscissa represents days, and the ordinate both specific conductivity and green weight of tops. The values given for conductivity should be multiplied by 10^{-5}

in order to get the specific conductivity values. In the case of the weights the numbers in the margin represent ten times the actual weight in grams, e.g., 40 in the margin = 4.0 grams.

From the results it is seen that both the increase in green

TABLE IX (Series 7)

GROWTH OF PLANTS AND CONDUCTIVITY OF FULL NUTRIENT MEDIUM FOR 50 DAYS

Cultures nos.	Length of period in full nutrient days	Av. green wt. of tops in each culture grams	Specific conductivity* at end of period		
			Minimum	Average	Maximum
1– 5	5	3.81	93.22	96.25	98.19
6–10	10	8.12	57.47	61.03	66.93
11–15	15	9.47	32.38	34.83	37.59
16–20	20	8.66	24.38	32.68	46.05
21–25	25	8.69	15.73	18.19	21.69
26–30	30	8.00	13.74	20.63	30.28
31–35	35	7.10	10.02	15.98	21.23
36–40	40	6.77	11.16	14.23	16.19
41–45	46	6.09	6.88	11.44	22.51
46–50	50	5.01	13.00	16.97	28.11

* The numbers in the three columns are to be multiplied by 10^{-5} in order to arrive at the specific conductivity values.

weight of tops and decrease in conductivity of the medium are most rapid and pronounced during the first 15 days. After that period both the green weight and the conductivity gradually decline, but the latter more slowly than the former. While the curves of the minimum, average, and maximum conductivity remain very close together during the first 15 days, they become more divergent after that time. The green-weight curve shows a gradual decline as the age of the plant increases, after a certain period, due to the drying of the tops and consequent loss of water. Different curves would, of course, have been obtained had the nutrient solution been renewed.

In table x and fig. 2 are seen the results of series 8, a similar experiment with distilled water, the same units being used as in the previous case. The green weight of tops increased during the first 10 days and then gradually declined to the end of the experiment. The conductivity of the water was practically the same on the 10th as it had been on the 5th day. Evidence from other experiments, however, indicates

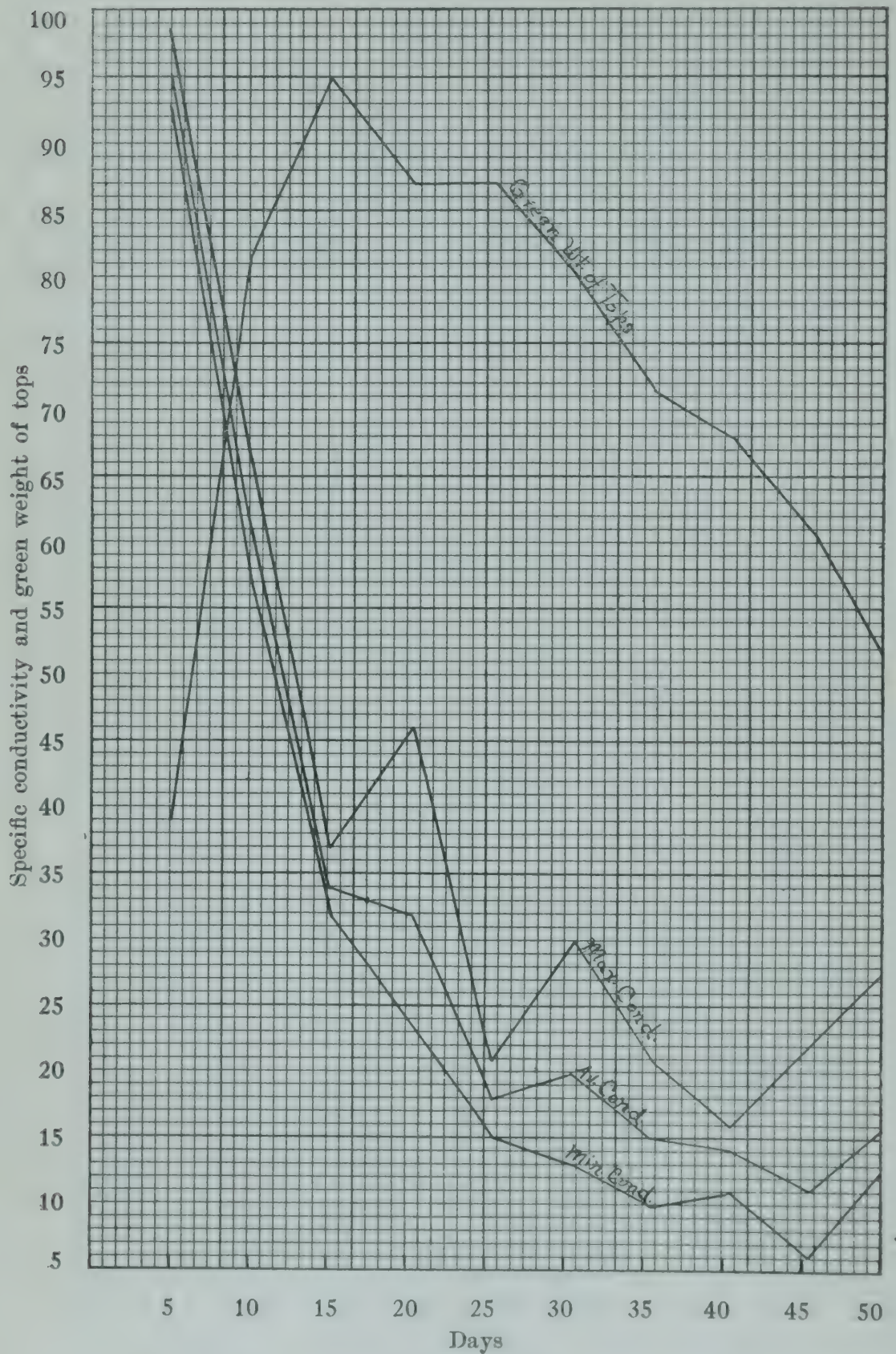

Fig. 1. The conductivity and growth curves for the full nutrient solution (Pfeffer's) in which plants were grown 50 days, the medium being unrenewed. (For complete explanation see the text.)

that in the interim the curve might have risen and fallen. After the 10th day the curve inclined with fluctuations. Here again are seen evidences that the 10-day period for seedlings in the distilled water may properly be considered a crucial one for the plants. After that time the growth declines and the conductivity increases markedly.

Suspecting that the question of injury to plants in distilled

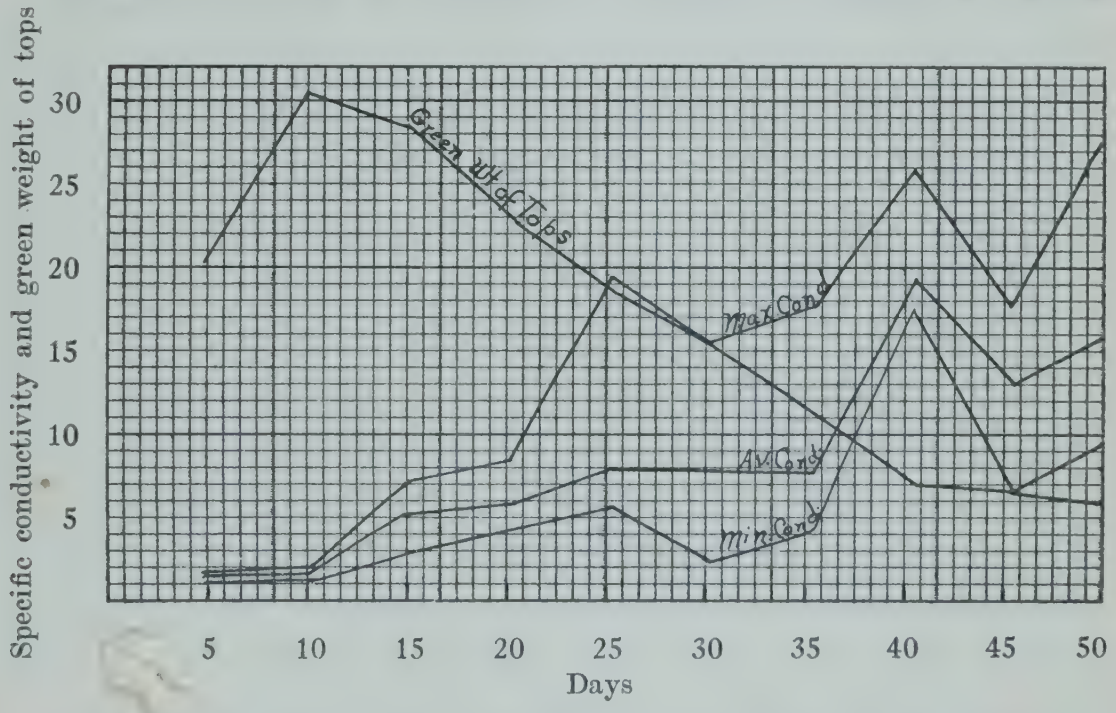

Fig. 2. The conductivity and growth curves for the unrenewed redistilled water in which pea seedlings were grown for 50 days. (For complete explanation see the text.)

water might be intimately bound up with that of lack of reserve food materials, the writer carried out an experiment bearing upon this matter. The experiment consisted, first, in placing some Canada field pea seedlings directly into redistilled water and determining the specific conductivity of the water at intervals for 20 days; and, next, in transferring some pea plants which had been grown in full nutrient solution for 1, 5, 10, 20, 30, and 40 days respectively to redistilled water, and determining the specific conductivity of the water at intervals for 20 days. The results are plotted as curves in fig. 3, the conductivity values being represented in terms of x on the Wheatstone bridge with a resistance of 9,110 ohms in the box. Four cultures of 10 plants each (except in the case

of the 20-day period in full nutrient solution in which 12 cultures were used) were grown under each of the specified conditions, and the curves represent the averages for the 4 (or 12) cultures under each condition. To determine how much

TABLE X (Series 8)

GROWTH OF PLANTS AND CONDUCTIVITY OF DISTILLED WATER MEDIUM FOR 50 DAYS

Cultures nos.	Length of period in dist. water days	Av. green wt. of tops grams	Specific conductivity* at end of period		
			Minimum	Average	Maximum
1– 5	5	2.04	1.46	1.54	1.66
6–10	10	3.07	1.01	1.34	1.81
11–15	15	2.89	3.04	5.43	7.41
16–20	20	2.34	4.34	5.92	8.63
21–25	25	1.89	5.66	8.15	19.77
26–30	30	1.55	2.60	8.26	15.82
31–35	35	1.15	4.43	7.80	17.95
36–40	40	.72	17.62	19.51	26.04
41–45	45	.68	6.87	13.32	17.95
46–50	50	.60	10.51	16.48	29.00

* The numbers in the three columns are to be multiplied by 10^{-5} in order to arrive at the specific conductivity values.

increase in conductivity was contributed by the glass tumblers in which the cultures were grown, 4 such containers filled only with redistilled water, and containing no plants, were used and the conductivity of the water determined at intervals for 20 days. It is seen that from the seedlings which had not been in full nutrient solution at all (Nos. 5–8) the highest conductivity resulted, while from those which were in the full nutrient solution longest before being placed in the distilled water (Nos. 37–40 and 33–36), the lowest conductivity was found at the end of 20 days. The other cultures at the end of 20 days were midway between the two extremes. It is also seen that, whereas the conductivity curve for Nos. 5–8 shows very little tendency to decline in the early stages, the curves for the cultures which had first been in full nutrient solution show that tendency to a considerable extent. And that tendency, as we have previously remarked, is a characteristic feature of normal plants transferred from full nutrient solution to distilled water.

Attention should be called to the difference in the character of the conductivity curves in fig. 2 and that of 5–8 in fig. 3. It

will be noted that both represent the conductivity curve of distilled water containing the roots of seedling peas. The difference mentioned no doubt finds its explanation in the different conditions under which the two series were grown (the series

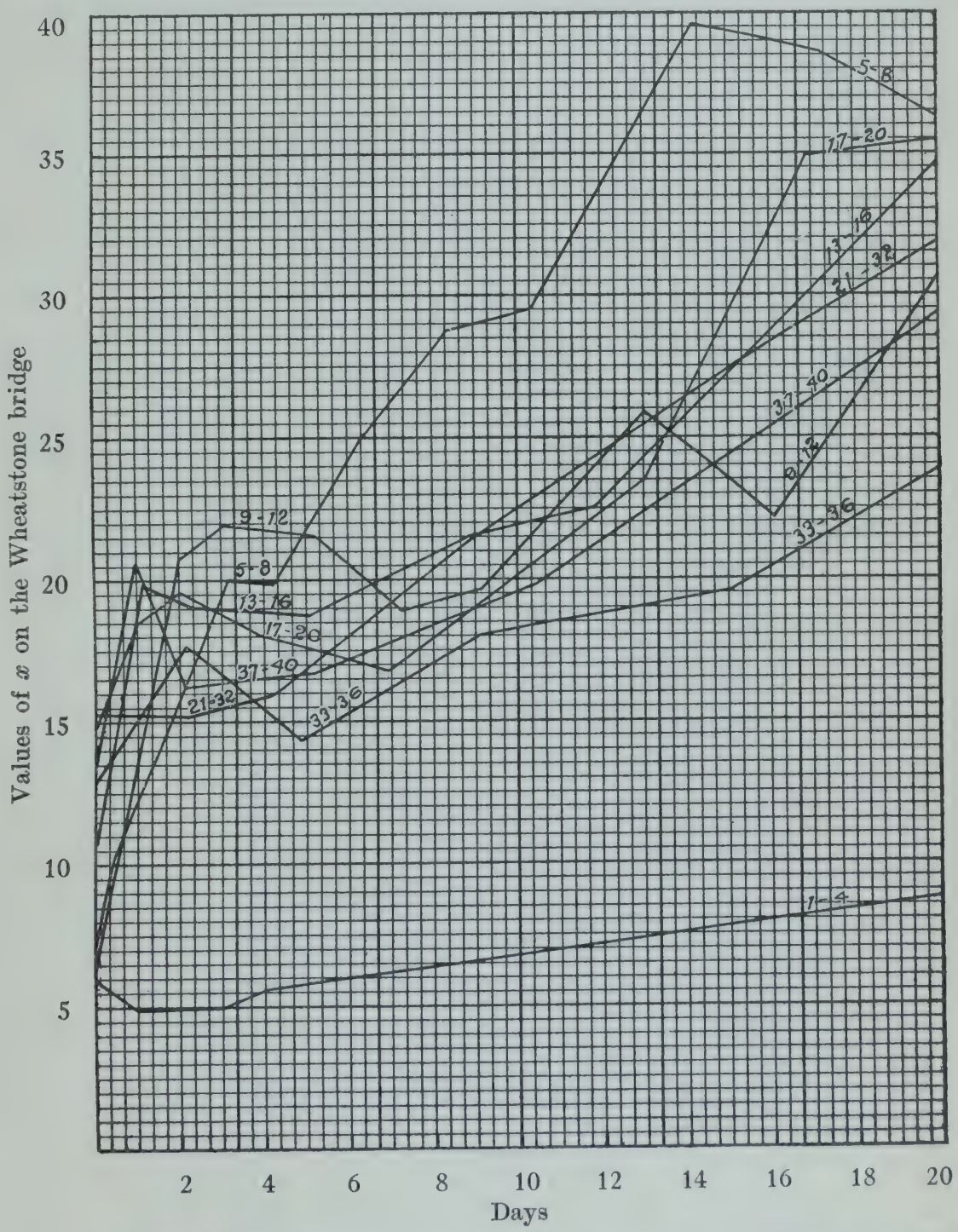

Fig. 3. The conductivity curves for cultures in distilled water 20 days—after growth in full nutrient solution for varying periods of time, as follows: Nos. 9–12, 1 day; Nos. 13–16, 5 days; Nos. 17–20, 10 days; Nos. 21–32, 20 days; Nos. 33–36, 30 days; Nos. 37–40, 40 days. Nos. 5–8 were grown only in distilled water, while Nos. 1–4 were without plants, consisting only of distilled water.

for fig. 2 being run in the fall when the seeds were fresh, and that for fig. 3 in the winter), in the vigor of the seeds, and in the difference in the units used in plotting the curves. It must be said, however, that various factors of the problem of exosmosis from the roots of plants remain as yet unknown.

The early drop in the curve of the conductivity of the controls (1–4) is an interesting feature which would seem to be explained by an adsorption of the electrolytes on the surface of the chemically clean glass tumblers.

At the end of 20 days in distilled water the roots of the plants which had not been in full nutrient at all showed marked deterioration (being badly decomposed and covered with a gelatinous coating), while the roots of those which had previously been in full nutrient solution for some time remained normal in every respect, even after 20 days in distilled water.

These results seem plainly to indicate that injury which plants sustain in distilled water is very closely related either to the lack of available nutrients in the medium or of reserve food material in the tissues. A seedling is in an exceedingly plastic state of growth. If no food materials become available the embryonic tissues which are in such an active condition of growth soon become disorganized, possibly suffering partial autolysis and becoming the prey to bacterial and fungous action. We would expect, therefore, that the larger the seeds (and hence also the supply of stored materials), the longer the seedlings could remain in distilled water before deterioration. Comparison of True's results on *Lupinus* with those here presented on *Pisum sativum* and *Vicia faba* seems to fulfill that expectation. We should also expect that the more nutrient materials the plant absorbed, the better it would be able later to withstand any deteriorating influences in the distilled water, and the experiment above noted seems to bear out that idea also.

In the light of what has been said we are led to believe that the conductivity curve of Nos. 5–8 is not a pure representation of exosmosis and that the products of bacterial and fungous action and cell decomposition account for at least a part of the conductivity. While the same condition may be

true of the other cultures to a certain extent, it no doubt plays a lesser, and real exosmosis a greater, part.

In connection with the above experiment it was thought desirable to determine whether a difference in the initial temperature of the water into which the roots were placed had any immediate or subsequent effect upon the exosmosis from the roots; plants which had been grown in full nutrient solution for 20 days were used for this purpose. Four cultures were prepared with distilled water at a temperature of 6.5°C., four at 17.2°C., and four at 35.0°C., and conductivity readings were taken after exactly one-half hour, and then at various intervals for 20 days. No attempt was made to keep the water at the initial temperatures and it therefore gradually returned to the temperature of the room. After one-half hour, when the first readings were taken, the respective temperatures were 8.9°C., 16.6°C., and 27.4°C.

The average conductivities of the water of these cultures are plotted for 20 days in fig. 4, the same units being used as in fig. 3. From these results it may be concluded that the initial differences of temperature can not be said to have exercised much, if any, effect. The results would probably have been different had the temperatures remained at the original point during the 20 days. Wächter ('05) has considered the rôle of the temperature factor in exosmosis.

VIII. Discussion and Conclusions

It is believed that the evidence furnished is sufficient to support the conclusion that pure distilled water *per se* is not toxic or injurious to plants, and that various other factors enter in to cause the deterioration noted when plants are placed in that medium.

Of course by qualifying the assertion to include *pure* distilled water only, we have thus eliminated the effect that may be produced by toxic substances in the distilled water, no matter from whence derived. The abundance of work that has been done on the toxicity of various substances to plant tissues would of course lead us to expect injurious effects if such substances were present in any quantity in the distilled

water. With that phase of the question we are therefore not much concerned at present. With a distilled water prepared as indicated, and with a specific conductivity which is approximately 2×10^{-6}, we have a water sufficiently pure for use in the consideration of other aspects of the question, and attention is directed to these.

The evidence presented has inclined us strongly to the view

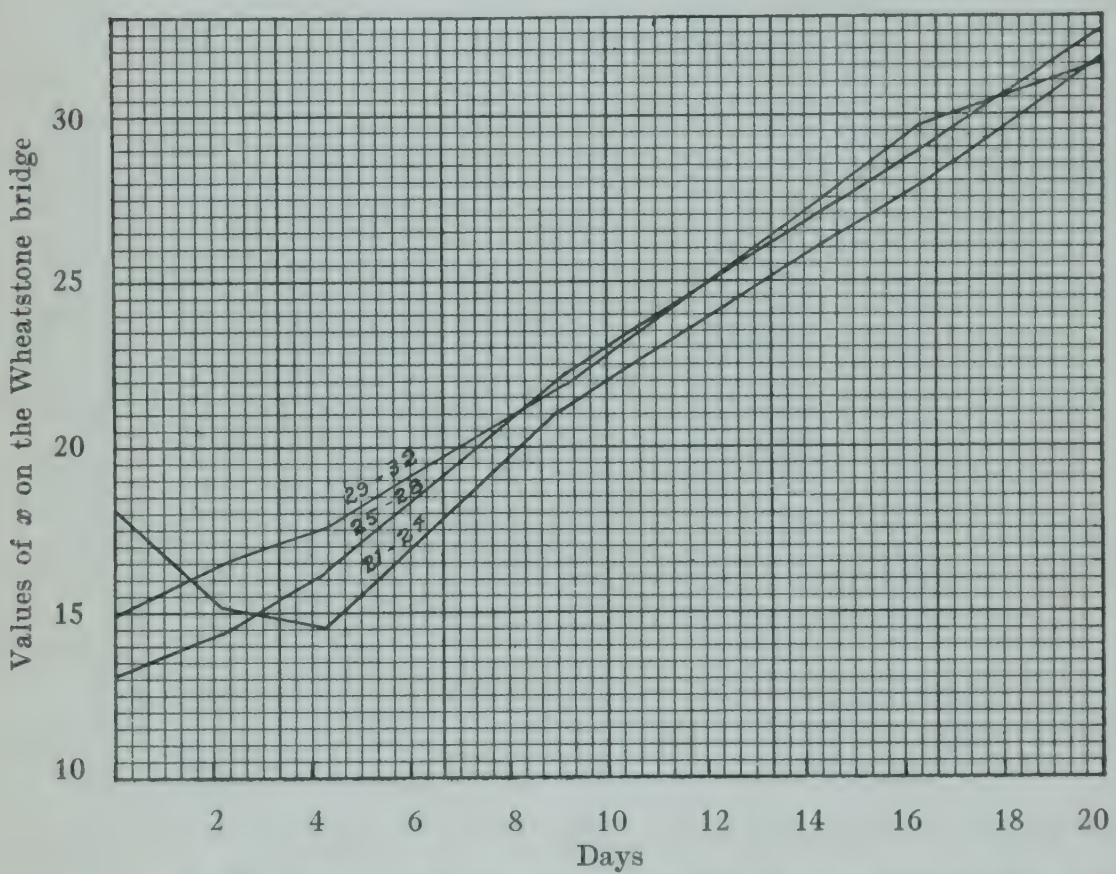

Fig. 4. The conductivity curves for cultures in distilled water 20 days—after growth in full nutrient solution for 20 days. The initial temperatures of the distilled water into which the roots were placed were as follows: Nos. 21–24, 6.5°C.; Nos. 25–28, 17.2°C.; Nos. 29–32, 35°C.

that the fundamental basis of the deterioration of plants in distilled water rests upon the food relations of such plants, but that, on the other hand, an exosmosis of food materials or nutrient salts is in no way responsible for the difficulty. It is considered that the question of the food relation plays an important rôle in the incipiency of the disorder, but that this is quickly followed by factors which have been initiated as a result of the inimical food or nutrient relation.

A plant must assuredly have food in order to thrive. The more food it has stored up in its tissues, the longer it can survive in a medium devoid of it. But because of the absence of available food it is believed that the tissues of the plant begin to become disorganized and in that condition fall a ready prey to bacterial and fungous action, which may then set in and play a very important part in the subsequent decomposition of the tissues.

While it may seem paradoxical to assert in one clause that absence of food is the fundamental basis of the injury which plants undergo in distilled water, and in the very next to say that exosmosis of nutrient salts plays no rôle, yet the results obtained have substantiated that idea. Furthermore, it is essential to consider the various other factors attendant upon these two conditions in order to arrive at the proper conclusions respecting their operation. Among such factors may be mentioned the decrease in conductivity after a short period coincident with exosmosis from normal tissues, the relation of sterilization to bacterial and fungous action, the recovery of plants under different conditions, and the numerous other questions already considered in the body of the article, all of which lend weight to the conclusions arrived at.

IX. Summary

A brief historical review is given in this paper of the views held in regard to the cause of injury to plants in distilled water.

The methods of work are outlined.

The experimental work is given and the results discussed, especially with reference to the conclusions of other workers.

A discussion is given of the results obtained in the experimental work and the conclusions derived therefrom are stated.

Some of the results obtained from the experimental work may be summarized as follows:

(a). Renewing the distilled water of the cultures every 4 days was in general beneficial, as shown by increased growth of both tops and roots. The plants were also able to survive longer in the renewed than in the unrenewed distilled water,

and continued growth better after being placed in a full nutrient solution.

(b). The period between 5 and 10 days in distilled water is a crucial one for plants; if they remain longer in this medium they are unable to recover normally or completely when subsequently placed in a full nutrient solution.

(c). By keeping the plants in distilled water a certain period before transferring to full nutrient solution the maturity of the plants is delayed.

(d). The longest period during which plants can be kept in distilled water and later recover on being placed in full nutrient solution was found to be 30–40 days. For certain dilute toxic solutions this period was much less, thus indicating that the so-called toxicity of distilled water is, if it exists at all, very slight.

(e). The lateral roots of "boundary cultures" were characteristically long and thread-like.

(f). Sterilizing the distilled water by boiling one-half hour every 4 days exercised a beneficial effect upon the growth of plants in that medium as compared with the growth of those in unsterilized distilled water.

(g). Greater total exosmosis was obtained in the renewed than in the unrenewed distilled water.

(h). Normal plants which have been grown for some time in full nutrient medium and then transferred to distilled water exhibit at first greater excretion than absorption of electrolytes. After one or two days, however, there is greater absorption than excretion and the conductivity curve declines. This condition may be maintained for a considerable period.

(i). The conductivity curve of the full nutrient solution in which plants were grown rapidly fell during the first 15 days or so; then it was more or less horizontal for a period, and finally began to incline after about 50 days. The growth curve was in general opposite in character to the conductivity curve.

(j). The conductivity of the distilled water in one series in which the roots of pea seedlings were placed was practically the same on the 10th as on the 5th day. After the 10th day

it rose considerably. The growth curve showed a rise the first ten days, then a decline.

(k). Higher conductivity in the distilled water after 20 days was caused by plants which had not previously been in full nutrient solution than by plants grown for a time in full nutrient solution before transference to distilled water. The former cultures also failed to give the decline in conductivity characteristic of normal plants transferred from full nutrient solution to distilled water.

(l). Greater deterioration of the roots in distilled water occurred if the plants had not previously been in full nutrient solution than in the case of plants which had been grown for a time in the latter medium.

(m). Initial difference of temperature of the distilled water produced no effect on the exosmosis of electrolytes.

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Explanation of Plate

PLATE 13

Figure 1.

Culture no.	Conditions of growth.
1	(2) *Unrenewed distilled H_2O, 45 days.
2	(3) Renewed distilled H_2O, 45 days.
3	(6) 1 day dist. H_2O, 44 days in renewed full nutr.
4	(8) 2 days dist. H_2O, 43 days in renewed full nutr.
5	(10) 5 days dist. H_2O, 40 days in renewed full nutr.
6	(14) 10 days dist. H_2O (renewed), 35 in renewed full nutr.
7	(18) 15 days dist. H_2O (renewed), 30 in renewed full nutr.
8	(22) 20 days dist. H_2O (renewed), 25 in renewed full nutr.
9	(23) 45 days in unrenewed full nutr.
10	(25) 45 days in renewed full nutr.

Figure 2.

1	(9) 5 days in unrenewed dist. H_2O, 40 days in unrenewed full nutr.
2	(10) 5 days in unrenewed dist. H_2O, 40 days in renewed full nutr.
3	(11) 10 days in unrenewed dist. H_2O, 35 days in unrenewed full nutr.
4	(12) 10 days in unrenewed dist. H_2O, 35 days in renewed full nutr.
5	(13) 10 days in renewed dist. H_2O, 35 days in unrenewed full nutr.
6	(14) 10 days in renewed dist. H_2O, 35 days in renewed full nutr.
7	(19) 20 days in unrenewed dist. H_2O, 25 days in unrenewed full nutr.
8	(20) 20 days in unrenewed dist. H_2O, 25 days in renewed full nutr.
9	(21) 20 days in renewed dist. H_2O, 25 days in unrenewed full nutr.
10	(22) 20 days in renewed dist. H_2O, 25 days in renewed full nutr.

* The numbers in parentheses correspond to the culture numbers of series 1. (See table 1.)

Fig. 1

Fig. 2

MERRILL—DISTILLED WATER

Explanation of Plate

PLATE 14

Figure 1.

Culture no.		Conditions of growth.
1	(2)	*33 days in unrenewed dist. H_2O at time picture was taken.
2	(3)	33 days in renewed dist. H_2O at time picture was taken.
3	(6)	1 day in dist. H_2O, 32 days in renewed full nutr.
4	(8)	2 days in dist. H_2O, 31 days in renewed full nutr.
5	(10)	5 days in unrenewed dist. H_2O, 28 days in renewed full nutr.
6	(14)	10 days in renewed dist. H_2O, 23 days in renewed full nutr.
7	(18)	15 days in renewed dist. H_2O, 18 days in renewed full nutr.
8	(22)	20 days in renewed dist. H_2O, 13 days in renewed full nutr.
9	(23)	33 days in unrenewed full nutr.
10	(26)	33 days in renewed full nutr.

Figure 2.

1	(9)	5 days in unrenewed dist. H_2O, 28 days in unrenewed full nutr.
2	(10)	5 days in unrenewed dist. H_2O, 28 days in renewed full nutr.
3	(11)	10 days in unrenewed dist. H_2O, 23 days in unrenewed full nutr.
4	(12)	10 days in unrenewed dist. H_2O, 23 days in renewed full nutr.
5	(13)	10 days in renewed dist. H_2O, 23 days in unrenewed full nutr.
6	(14)	10 days in renewed dist. H_2O, 23 days in renewed full nutr.
7	(19)	20 days in unrenewed dist. H_2O, 13 days in unrenewed full nutr.
8	(20)	20 days in unrenewed dist. H_2O, 13 days in renewed full nutr.
9	(21)	20 days in renewed dist. H_2O, 13 days in unrenewed full nutr.
10	(22)	20 days in renewed dist. H_2O, 13 days in renewed full nutr.

* The numbers in parentheses correspond to the culture numbers of series 2. (See table III.)

Fig. 1

Fig. 2

MERRILL—DISTILLED WATER

Explanation of Plate

PLATE 15

Figure 1.

Culture no.		Conditions of growth.
1	(1)	*10 days in unrenewed dist. H_2O, 42 days in unrenewed full nutr.
2	(2)	10 days in unrenewed dist. H_2O, 42 days in renewed full nutr.
3	(3)	10 days in renewed dist. H_2O, 42 days in unrenewed full nutr.
4	(4)	10 days in renewed dist. H_2O, 42 days in renewed full nutr.
5	(5)	20 days in unrenewed dist. H_2O, 32 days in unrenewed full nutr.
6	(6)	20 days in unrenewed dist. H_2O, 32 days in renewed full nutr.
7	(7)	20 days in renewed dist. H_2O, 32 days in unrenewed full nutr.
8	(8)	20 days in renewed dist. H_2O, 32 days in renewed full nutr.
9	(9)	30 days in unrenewed dist. H_2O, 22 days in unrenewed full nutr.
10	(10)	30 days in unrenewed dist. H_2O, 22 days in renewed full nutr.
11	(11)	30 days in renewed dist. H_2O, 22 days in unrenewed full nutr.
12	(12)	30 days in renewed dist. H_2O, 22 days in renewed full nutr.
13	(13)	40 days in unrenewed dist. H_2O, 12 days in unrenewed full nutr.
14	(15)	40 days in renewed dist. H_2O, 12 days in unrenewed full nutr.

Figure 2.

1	(1)	†32 days in unrenewed dist. H_2O.
2	(2)	32 days in renewed dist. H_2O.
3	(20)	32 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$.
4	(22)	1 day in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 31 days unrenewed full nutr.
5	(23)	2 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 30 days unnewed full nutr.
6	(24)	4 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 28 days unnewed full nutr.
7	(25)	8 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 24 days unrenewed full nutr.
8	(26)	12 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 20 days unnewed full nutr.
9	(27)	16 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 16 days unrenewed full nutr.
10	(28)	20 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 12 days unrenewed full nutr.
11	(29)	32 days in unrenewed full nutrient solution.

*The numbers in parentheses correspond to the culture numbers of series 3. (See table v.)

†The numbers in parentheses correspond to the culture numbers of series 4. (See table vi.)

Fig. 1

Fig. 2

MERRILL—DISTILLED WATER

Explanation of Plate

PLATE 16

Figure 1.

Culture no.		Conditions of growth.
1	(1)	*30 days in unrenewed distilled H_2O.
2	(2)	30 days in renewed distilled H_2O.
3	(3)	30 days in distilled H_2O, sterilized every four days.
4	(4)	30 days in distilled H_2O, sterilized every four days.
5	(5)	30 days in unrenewed full nutrient solution.
6	(6)	30 days in renewed full nutrient solution.

Figure 2.

Showing the method used for seed germination.

*The numbers in parentheses also correspond to the culture numbers of series 5. (See table VII.)

Fig. 1

Fig. 2

ELECTROLYTIC DETERMINATION OF EXOSMOSIS FROM THE ROOTS OF PLANTS SUBJECTED TO THE ACTION OF VARIOUS AGENTS

M. C. MERRILL

Formerly Research Assistant to the Missouri Botanical Garden

I. Introduction

In a previous paper the writer ('15) gave some results showing the exosmosis curves when normal growing plants are taken from a full nutrient medium and placed in redistilled water. Those results and the data herewith given show that exosmosis of electrolytes is a constant feature associated with the transfer of normal growing plants from a full nutrient solution to distilled water. In the paper above mentioned evidence was introduced indicating that such exosmosis was not a causal injury but that it was simply a concomitant condition or incidental effect and had but an indirect relation to the inimical condition of the plant in the distilled water. For convenience we might designate the agency or agencies causing such exosmosis as *passive* in their effects.

In this paper are given results on exosmosis in terms of the electrolytic conductivity of the medium when such excretion is caused, or at least is accelerated, by various factors or agencies which we may designate as *active* in their effects. Accordingly, plants have been treated by injurious agents or subjected to conditions of different kinds and the comparative effects on the exosmosis from the roots have been noted. By determining the conductivity of the medium at various intervals subsequent to the treatment, data have been secured for plotting the exosmosis curves shown in this paper. It has also been the aim to determine in each case the approximate boundary between the normal and the abnormal exosmosis by varying either the duration of application or the concentration of the substance applied, or both. Hence in most cases there will be found the two extremes with any given substance—at the upper end of the scale the curve of excessive exosmosis due to

cytolysis or death of the cells (though it should be noted here that excessive exosmosis from the roots may result even when those tissues are in an apparently normal condition), and at the lower end of the scale the curve of slight exosmosis that is in the region of the normal curve of exosmosis for untreated plants placed from full nutrient solution into distilled water. Between these two extremes lie various gradations depending on conditions.

II. Historical Review

The work that has been done on the problem of excretions from the roots of plants is very interesting from several standpoints and has been considered by various workers to be of great practical importance. Nearly a century ago De Candolle ('32) advocated a theory of crop rotation on the basis of root excretions in which he claimed that certain plants excreted from their roots substances which are harmful to succeeding crops of closely related plants, but not so to plants less closely related. This theory was based partly on his own observations and partly on the statements of earlier workers.

At De Candolle's suggestion Macaire ('32) performed some experimental work pertaining to root excretions. He took plants from the soil, washed the roots carefully, and placed them in rain water. After several days, during which the water was frequently changed, the water was yellow and had odor, taste, and chemical reactions indicative of contained exuded materials. By placing one part of the roots of a plant in a vessel of pure water and another part in a second vessel containing a solution of lead acetate and later finding the salt in the pure water, he concluded that a plant can excrete a poison which it has absorbed. The results of Macaire's experiments with water cultures led him to favor the theory of crop rotation on the basis of the excretions from the roots of plants, as advanced by De Candolle.

Braconnot ('39) repeated many of Macaire's experiments but was unable to convince himself that plants excrete toxic substances from their roots, and hence he did not look with favor upon De Candolle's theory. Braconnot believed that

capillary action played a rôle in Macaire's experiments whereby he obtained an excretion of lead acetate into distilled water, as noted above. Boussingault ('45) considered that under ordinary conditions radicular excretion is doubtful, and that any excretion from the roots in water is caused by disease. He also advanced various arguments opposing De Candolle's theory.

Gyde ('47) grew various agricultural plants in soil for a time and then, after carefully washing the roots, placed them in pure water. After 3–17 days, during which the plants continued in good condition for the most part, the water was evaporated. The finding of a residue of yellowish or brown matter, part organic and part inorganic, caused him to conclude that plants excrete both organic and inorganic substances in minute quantities, similar in composition to the sap. But he denied that root excretions have any injurious effect upon plants later grown in the same medium.

An examination of the literature on the subject of root excretions reveals the tendency among the workers of the particular period at which we have now arrived in our review, to pay more attention to the morphological and chemical aspects of root excretions, and perhaps not so much to the purely agricultural phases. Hence we find from this period on, considerable emphasis laid on the structure of the root and a more detailed account given regarding the chemical nature of the substances excreted from the roots, even though the experimental methods were somewhat crude in most cases. Furthermore, it should be said that opinion was divided on the question of whether or not there is an actual excretion from the roots.

Among those whose influence was felt in the development of the chemical aspects of the subject at this time Liebig should probably be mentioned first. In the American edition of his work ('41, p. 195) occurs the following statement: "It is evident that plants, also, by producing carbonic acid during their decay, and by means of the acids which exude from their roots in the living state, contribute no less powerfully to destroy the coherence of rocks." An appended note by Dr. Webster in the

same work ('41, p. 411) says that other chemists were unable to obtain results similar to those of Macaire. If they did, they were inclined to ascribe them to injury of the roots examined.

Various workers were thus attacking different phases of the problem. Chatin ('47) mentioned the excretions from roots and especially considered the elimination of toxic substances by them. Link ('48) held that the slimy drops found on root tips should not be considered as actual excretion inasmuch as they arise from the cast-off cap cells of the root. Garreau and Brauwers ('58) maintained a similar view in regard to the gummy, nitrogenous substance they found given off by the roots to the water in which they were placed. The observations of Liebig ('58) concerning the dissolving action of roots on limestone were later substantiated by the experimental work of Sachs ('60), which has been so much referred to since that time. Of the two possible explanations Sachs advanced —excretion of carbonic acid by the roots, and the liberation of acids by the decomposition of the cell walls of the roots—he inclined to favor the latter as being the best explanation for the marble etchings caused by the roots in his experiments. In his extensive series of experiments, Knop ('60, '61, '62) studied, among other things, the character and amount of root excretions from certain plants placed in distilled water, and the conditions governing the same. His analyses indicated that, in addition to other substances in small amounts, potassium, calcium, phosphoric acid, and some organic matter were excreted. The studies of Cauvet ('61) resulted in his declaring that physiologically sound roots do not excrete any substances, toxic or otherwise, and that all theories based on the ideas of root excretion advanced by De Candolle and Macaire were necessarily false. Sachs ('65) made further contributions along his line of work indicated above, while Liebig ('65) says:

> "Wir haben allen Grund zu glauben, dass diese Absonderung an der ganzen Oberfläche stattfindet, wir beobachten sie nicht nur am Stamme, sondern auch an den kleinsten Zweigen, und wir müssen daraus schliessen, dass dieser Excretionsprocess auch an den Wurzeln vor sich geht. . . . . Eine Ausscheidung von Excrementen kann demnach bei den Pflanzen

nicht geleugnet werden, wiewohl es möglich ist, dass sie nicht bei allen Pflanzen in gleichem Grade stattfindet."

Molisch ('87) branched out in a new direction as regards the subject of root excretions; he held that such excretions exercise an influence on organic bodies in the soil which is even more important than that exercised upon the inorganic constituents of the same, for he considered the latter merely a dissolving action but the former a real chemical transformation. His main work along this line pertained to a study of the ferments in the root excretions, and their reactions and properties. Johnson ('90), after considering Gyde's results above noted, says that "we may well doubt whether agricultural plants in the healthy state excrete any solid or liquid matters whatever from their roots," but that "under certain circumstances, small quantities of soluble salts or free acids may indeed *diffuse* out of the root-cells into the water of the soil. This is, however, no physiological action, but a purely physical process." Goebel ('93) found that after the roots of Hordeum and Lepidium plants had been in distilled water for six days the medium gave the reaction for formic acid.

We thus see that the early work on root excretions was characterized by contradictions and uncertainties. While the nature of the more recent work has been more exact and comprehensive, the subject, as we shall see, is still beclouded by a considerable degree of confusion.

A classic piece of experimental work was undertaken by Czapek ('96, '96[a]) to determine the exact chemical nature of the excreted substances from roots. In his report ('96[a]) he discussed the earlier work, especially with regard to the relation between excretion from injured cells and actual exosmosis. In his experimental work he found that root excretions are composed of soluble substances, partly organic and partly inorganic. Of the inorganic, he identified K, Ca, Mg, HCl, H_2SO_4, and H_3PO_4, only the first and last mentioned—in the form of the primary potassium phosphate—being excreted in any quantity. Of the organic substances he identified carbonic acid and also formic acid, the latter in the form of its potassium salt; oxalic acid was also isolated as a primary

potassium salt. Czapek believes the reddening of litmus paper by root excretions to be due ordinarily to the acid reaction of monopotassium phosphate, but in the case of hyacinth roots to the primary oxalate. The corrosion of marble he attributed to the dissolving effect of carbonic acid. While considering as possible the results obtained by Molisch ('87), who claimed that diastatic ferments were normally present in the root excretions, Czapek's own work in repetition of Molisch's experiments offered only negative results.

Prianischnikov ('04) performed some experimental work dealing with the action of organic acids on phosphates. It will be remembered that because the roots did not attack aluminum phosphate Czapek concluded that organic acids were not excreted by them, inasmuch as this substance is soluble in certain organic acids. Prianischnikov found that phosphates derived from different sources were utilized by various plants but in different degree, and he suggested that this might be correlated with a different amount of CO_2 excretion, in which case the presence of organic acids would not be necessary.

Kunze ('06) found that free mineral acids are not excreted from the roots of higher plants and concluded that any acidity in the excretions is probably not due to the presence of acid salts of mineral acids, but to excreted organic acids. These, however, were present in such minute amounts as to be below the sensitiveness of litmus. He held that a greater effect is produced on the soil by fungi than by the roots of the higher plants. Lemmermann ('07) held views similar to those of Kunze.

Stoklasa and Ernest ('08) disagree with the findings of both Czapek and Kunze. No potassium or phosphoric acid were ever found as a result of their determinations, and they maintain that in the economy of the plant the excretion of such useful or necessary substances is unthinkable. Only CO_2 was found to be excreted under conditions of normal aerobic respiration of the root system; no other free inorganic or organic acids were detected. In aerobic respiration of the root system, they believe the organic acids in the living cells would be split up to give CO_2 and H_2, the latter then being oxidized to H_2O.

They determined the amount of CO_2 excretion per gram dry weight of roots of wheat, oats, rye, and barley. The amount varied for the different plants but a correlation was found between the amounts of P_2O_5, K, and Na contained in the dry roots of plants grown on gneiss and basalt and the amount of CO_2 excreted.

We now come to the work of various soil investigators whose results have again focused attention during the past decade upon De Candolle's original theory. The essential features of this work have become so well known that for our purpose it is not necessary to do much more than merely mention it here. Though not considering directly the phases of the subject with which we are dealing, yet the much-discussed paper by Whitney and Cameron ('03) is historically important and bears an intimate relation to the later work of the investigators in the Bureau of Soils of the U. S. Department of Agriculture, the results of which led to the so-called toxic-excretion theory. Among the workers most prominently connected with the early studies along this line may be mentioned Livingston, Britton, and Reid ('05); Livingston, Jensen, Breazeale, Pember, and Skinner ('07); Schreiner and Reed ('07); Schreiner, Reed, and Skinner ('07); Schreiner and Reed ('07[a]); and others. As is well known, opinion is much divided on the various phases of this subject, however. Among those opposing the ideas or theories advanced along this line by the investigators named above should be mentioned Hopkins ('10); Hall, Brenchley, and Underwood ('14); and others.

That the question is one upon which investigations are still being pursued is shown by the publications from various quarters. As recent examples of these the work of Molliard ('13) and Prianischnikov ('14) may be cited. The former found that peas grown in water cultures in which previous crops of peas had grown produced a smaller growth than the original crops. This he attributed to the excretion of toxic substances in the medium by the earlier plants. The latter, from his own experimental work and from the results observed by him at the Rothamsted Experiment Station, is inclined to believe that the hypothesis of root excretion is not sufficiently demon-

strated. He says that other factors, as, for example, the physical nature of the soil, decomposition of roots, change in reaction of soil, etc., might be supposed to accomplish the same results as toxic excretions from the roots. In pure distilled water he found no decrease in either the size or quality of the crops of the second and third plantings, either where wheat followed wheat or where wheat followed oats. Experiments in sand, however, showed great decrease in the amount of the harvest of the second and third crops, but this, he believes, might be explained by the operation of the above-named factors.

So much for root excretions; we now come to a general consideration of exosmosis from living cells, both under natural conditions and under treatment of different kinds. While a great deal of attention has been given in the past to the intake, or endosmosis, of substances by the cell from its surrounding medium, comparatively little has been done on the opposite effect—the outgo, or exosmosis, of substances from the cell. It should be said, however, that the latter process, both in extent and in importance, is no doubt of much less significance in the plant's economy than the former.

Sachs ('60[a]) referred to the exosmosis of soluble material from germinating seeds when they remain for some time in distilled water. Knop ('64), in his studies on the absorption of salts by healthy seeds, also determined the quantities of the different salts which pass out of the seeds during the time they are swelling in distilled water. He found that both organic and inorganic substances were excreted. Hofmeister ('67) ascertained that when fresh pieces of sugar-containing plants were placed in water, no sugar passed out of the tissues into the medium. The much-cited experiments of De Vries ('71) showed that pieces of red beet placed in water for 15 days gave no trace of sugar or of colored material to the water during that time. In a NaCl solution of sufficient concentration, however, he obtained an exosmosis of both sugar and colored material. Turnips, beets, and the seedling roots of wheat, barley, and corn were used in the experiments of Boussingault ('74) but from none of them did he detect any

exosmosis of sugar into the water in which they were placed. Pfeffer ('76, '77) and Detmer ('79) also confirmed the results above noted regarding the absence of sugar in the water in which roots or other plant parts had been exposed for some time. Wilson ('81) found that in some cases (*Dionaea* and *Drosera*) the excretions may be influenced by external factors, e. g., partly by irritation caused by nitrogenous substances and partly by osmotic action. In general, he believed that the excretion of nectar is caused by the osmotic action of a fluid on the surface of the nectary. Pfeffer ('86) studied the effects of various organic acids (citric, picric, and tannic) and some inorganic compounds in causing the exosmosis of absorbed methylene blue from *Lemna, Trianea, Azolla,* and *Elodea.*

Wächter ('05) obtained considerable exosmosis of sugar, especially in the case of *Allium Cepa*; he found, however, that salts like NaCl and KCl tended to inhibit this exosmosis. He also investigated the effect of ether on this phenomenon. While he obtained greater exosmosis of sugar the first two days in a solution of ether alone than in one of ether and KCl, he attributed this increase to leaching from cells killed as a result of contact with ether, and believed that the ether itself has no effect on the actual process of exosmosis.

Lepeschkin ('06), from his experimental work on sporangia of *Pilobolus,* concluded that the exosmosis of water was due to an alteration of the plasma membrane caused by the anesthetics he used, provided the amounts employed were sufficient to be toxic. Small amounts of ether and chloroform, on the other hand, were found to decrease the exudation of water, and he believed this to be due to a decrease in permeability of the plasma membrane.

An interesting line of investigation was undertaken by Czapek ('10, '10[a], '10[b], '11) a few years ago to determine the surface tension relations of the plasma membrane. That work is especially pertinent to our discussion here because of the prominent part exosmosis played in his experiments. He used for the most part species of *Echeveria, Spirogyra,* and *Saxifraga,* in the cells of which is found a tannoid substance,

anthocyan, which is precipitated by caffein, giving a loose compound of tannin and caffein, called a "myelin-formation." Ammonia also gives this precipitate even in a solution as dilute as 1–15,000. Czapek investigated the effect produced by the application of a great variety of organic compounds and some inorganic acids in varying dilutions and for different periods of time, and determined the concentration at which exosmosis just occurred, i. e., the critical point. At the higher concentrations exosmosis of the tannoid substance readily occurred, as shown by the absence of the "myelin-formation" when caffein or ammonia was subsequently added. At the lower concentrations exosmosis did not occur and a precipitate was obtained, while at the critical point the precipitate was barely visible and usually in the form of fine particles.

By the use of his "capillar-manometer," Czapek was able to measure the surface tension exerted by the various concentrations, and found that, considering the surface tension of water as unity, that of the critical concentrations was approximately .68 in most cases. This lowering of the surface tension he considered as essentially a physical phenomenon which is intimately connected with the osmotic activities of the plasma membrane and is to be differentiated from the toxic action of injurious substances, e. g., anesthetics, whose action is chemical in large part, since even in very dilute solutions these caused marked exosmosis. Czapek used both aqueous and colloidal solutions and found that in general the critical concentrations had a surface tension of .68 in terms of water as unity. Inversely, he therefore concluded that the surface tension of the plasma membrane was also approximately .68 for the plant cells investigated. In his study of acids he found results coincident with those of Kahlenberg and True ('96) in that N/6400 was the critical concentration for exosmosis of the tannin bodies, just as those workers had found it to be the critical concentration for growth of Lupinus seedlings in solution culture.

In his later experimental work Lepeschkin ('11) obtained additional evidence tending to confirm and add to his previous results, as mentioned above. Thus he found that aniline dyes

penetrated cells of *Spirogyra* more slowly in the presence of one per cent chloroform than when the anesthetic was not used. If the cells were killed by the narcotic the rate was the same as for normal cells. He also used *Tradescantia discolor* and by the plasmolytic method found that the permeability to KNO_3 decreased during narcosis. This he explained on the assumption that the anesthetics (chloroform and ether) accumulated in the disperse phase of the plasma membrane which thereby leads to a hindrance of the solubility of KNO_3 and aniline dyes in the same. He considered that his results therefore showed that Nathansohn's hypothesis regarding the mosaic structure of the plasma membrane is not correct.

Another important piece of work dealing with the phenomenon of exosmosis from living tissue is that accomplished by Lillie ('09, '10, '11, '12, '12[a], '13, '13[a], '13[b]) and discussed at length in his various papers. Among other things he worked on the larvae of *Arenicola* and the eggs of *Arbacia,* each of which contains a pigment, and found that on placing them in NaCl or KCl solution (.55m) isotonic with sea-water, there was a rapid exosmosis of the contained pigment into the surrounding medium. When, however, the organisms were placed in the salt solutions to which had previously been added in a certain concentration any one of several anesthetics belonging to various classes (alcohols, esters, hydrocarbons, and miscellaneous compounds) a checking or possibly a complete prevention of exosmosis resulted. In general, all the anesthetics tried gave cytolysis in strong concentrations and therefore a rapid exosmosis of the pigment, while in weaker concentrations they showed a definite protective or anticytolytic action against the salt solution when used in conjunction with it. Lillie finds the explanation of the observed phenomenon in the relations of the plasma membrane, the salt solutions used having a permeability-increasing action which is offset or prevented by the temporary alteration of the membrane as the result of the action of the anesthetic. The alteration, he believes, is accompanied by an increase in the volume of the lipoid particles of the membrane.

In connection with the general subject of exosmosis it might

be well briefly to mention the results obtained by some of the earlier investigators working on the products excreted by the leaves of plants. De Saussure (1804) found that leaves immersed in distilled water soon lose a considerable amount of substance, composed for the most part of alkaline salts. Treviranus ('38) mentioned the results of various workers who studied the incrustation of minerals on the surface of leaves and found it to consist of calcium and silicon salts, especially of calcium carbonate. Gaudichaud ('48) and Payen ('48) both found that there is an alkaline excretion on certain parts of the leaves of some plants, yet they disagreed as to the extent of this phenomenon in nature. Sachs ('62) ascertained that drops of water on the leaves of certain plants soon become alkaline, which he considered to be the result of an outward diffusion of alkaline salts in the leaf. Volkens ('84) studied the deposit of calcium carbonate found on the leaves of various plants. Dandeno ('02) made a comprehensive study of the different phases of the subject. Among other things, he determined that the alkaline substances extracted from leaves by distilled water are largely potassium and calcium carbonates and probably potassium oxalate. He further found that the residue from the evaporation of dew drops, guttation drops, and of water used in drenching the leaves is practically the same, and is similar to the calcareous deposit found upon the leaves of certain plants. The above investigations may therefore be considered as tending to substantiate the idea of exosmosis from leaves.

III. Methods of Experimentation

The methods used for the electrolytic determination of exosmosis were the same as those described in the writer's paper referred to above. In that contribution (Merrill, '15) some of the curves were plotted on the basis of the specific conductivity. In the present paper, however, all curves are plotted on the basis of the values of x on the Wheatstone bridge when the resistance in the box is 9,110 ohms; as these values increase the specific conductivity also increases. In order to have a basis of comparison between the values of x

and the specific conductivity, the corresponding values of the latter for the values of x at 5, 10, 25, 50, 75, and 85 are given herewith:

Values of x on Wheatstone bridge for resistance of 9,110 ohms.	Corresponding values in terms of specific conductivity (to be multiplied by 10^{-5})
5	.23
10	.49
25	1.49
50	4.48
75	13.46
85	25.43

It is also advisable to have the conductivity values represented in terms of the concentration of some salt. The following are the values of the specific conductivity of NaCl solutions at 25° C. which had been determined by the writer for the concentrations indicated:

Concentration of NaCl	Specific conductivity (to be multiplied by 10^{-5})
N/16	686.13
N/32	353.94
N/64	181.93
N/128	93.25
N/256	47.79
N/512	24.54
N/1024	12.60

The correction for the specific conductivity of the water itself is not considered in the above values. Neither is that correction applied in any of the work here reported, since it is always a constant factor and only relative values are desired for the most part.

Plants of *Pisum sativum* were used. For the method of growing the seedlings, and other manipulations, see the writer's paper referred to (Merrill, '15). The plants were grown in full nutrient solution until a vigorous or well-developed condition was attained and then they were transferred to redistilled water[1] after rinsing the roots carefully and thoroughly in once-distilled water. Ten plants were grown in each culture. The treatment was always given when the plants were either in distilled water or in the solution, the effects of which on the plants were being studied. In all cases where the read-

[1] Hereafter, throughout this paper, whenever "distilled water" is referred to it will be understood to mean redistilled water with a specific conductivity of approximately 2×10^{-6}. If the ordinary distilled water is referred to, it will be specially designated as "once-distilled water" or some such distinguishing term.

ings were made in the distilled water, the resistance in the resistance box was 9,110 ohms. In some media other resistances were used; in such cases the values are given only in tables, and in terms of specific conductivity.

TABLE I

EFFECTS OF VARIOUSLY TREATED PLANTS ON THE DISTILLED WATER MEDIUM AS SHOWN BY GROWTH OF SECOND CROP

Culture no.	Kind and duration of treatment	Green wt. of tops of 2nd crop* grams
1 and 2	Controls—no treatment; full nutrient to dist. H_2O	2.90
3	Plant tops packed in ice 19 hrs.; dist. H_2O unchanged	2.80
4	Plant tops packed in ice 19 hrs.; dist. H_2O changed	2.80
5	In gas incubator at 50°C., 3.5 hrs.	1.60
6	In gas incubator at 50°C., 3.5 hrs.	2.55
7 and 8	Inoculated with *Ascochyta Pisi*	2.80
9	Illum. gas under bell jar, 6 hrs.; dist. H_2O unchanged	2.75
10	Illum. gas under bell jar, 6 hrs.; dist. H_2O changed	2.25
11 and 12	N/1 $MgCl_2$ in full nutrient as the solvent, 7 hrs.	5.20
13 and 14	.5% H_2SO_4 in full nutrient as the solvent, 7 hrs.	2.30
15 and 16	1% KOH in full nutrient as the solvent, 7 hrs.	8.45
17 and 18	Plants grown throughout in dist. H_2O; replaced by fresh seedlings in the unrenewed dist. H_2O	2.55
19 and 20	Same as Nos. 17 and 18, except that second crop was horse beans	6.85
21 and 22	Canada field peas in fresh dist. H_2O; no second crop	2.82
23 and 24	Horse beans in fresh dist. H_2O; no second crop	8.15

* The 2nd crop was 27 days old at time of weighing.

IV. Preliminary Experiments

In order to determine in a preliminary way whether the exosmosis from the roots of plants seriously affected by injurious agencies was sufficient to noticeably influence a new crop of seedlings in that medium (distilled water plus the excreted substances) as compared with control cultures in pure distilled water, the following series was set up. Canada field pea seedlings were grown in full nutrient solution until they were 15 days old, at which time they were about 8 inches high, and were green, vigorous, healthy, and in good condition. They were then treated in accordance with the plan given in table 1. In some cases, depending on the nature of the agent applied, the treatment was given after the plants had been transferred to distilled water. This was the case with Nos. 3, 4, 5, 6, 9 and 10. Cultures 7, 8, and 11–16 were treated while still in the

full nutrient medium, after which they were transferred to distilled water. In all instances, however, the roots were carefully rinsed before being placed in the water.[1]

To determine if any impurities had contaminated the distilled water in the cultures treated with ice, the distilled water in No. 4 was renewed after the operation. The resulting crop, however, was practically the same in cultures 3 and 4 and hence it may be considered that no plant food had entered from the ice. The distilled water was renewed in No. 10 a few hours after the treatment. The result of so doing was to discard the plant foods already excreted during, and immediately after, the treatment. This fact was evident from the better growth of the plants in No. 9 as compared with those in No. 10. Later work also showed that exosmosis caused by treatment with illuminating gas and other agents is comparatively rapid and immediate.

After the treatment the plants remained in the distilled water for 5–6 days, after which they were discarded. The distilled water level was then raised to the original height by adding fresh distilled water, and into this medium fresh Canada field pea seedlings were placed and the resulting growth determined. Cultures Nos. 17–24 are given in table 1 for comparison. After pea seedlings had been grown for 21 days in the unrenewed distilled water of cultures 17–20, the original plants were discarded and fresh seedlings of peas and horse beans were placed in the same distilled water. For comparison, cultures of these plants (Nos. 21–24) were set up at the same time in fresh distilled water.

Returning now to the effects of the treatments on the plants and noting the results given in table 1, we see marked differences evident. Neither the ice nor the inoculation with *Ascochyta Pisi*[2] produced any effect either on the plants or on the excretions from their roots, and hence these cultures are sim-

[1] The usual method of rinsing throughout this work was as follows: The solution to be discarded was thrown out, the tumbler filled twice with once-distilled water (the roots replaced and the whole thoroughly shaken each time), and then distilled water (redistilled) was added, the roots replaced, and the readings taken.

[2] Cultures of *Ascochyta Pisi* were kindly supplied the writer by Dr. R. E. Vaughan.

ilar and comparable to the untreated controls. Marked injury resulted in the case of the heat, illuminating gas, $MgCl_2$, and H_2SO_4, all in characteristic manner. The injury from KOH was rather slow in manifesting itself, but the coloration of the roots was a noticeable feature. An interesting condition to be noted here, which holds true also in the later experiments, is in regard to the effect of the heat and the illuminating gas. It should be borne in mind that during these treatments the roots remained in water. The tops only were affected and died; the roots remained white, turgid, and normal in appearance even though the exosmosis from them had been excessive, thus indicating a transfer of some electrolytes from the tops and down into the medium through the roots. Later experiments also substantiated the fact that abundant exosmosis sometimes occurs from roots which remain normal in appearance. The other agents ($MgCl_2$, H_2SO_4, and KOH) caused more or less injury to both tops and roots. The exosmosis of nutrients into the water from the affected plants is evident by the greater growth of fresh pea seedlings placed in such water as compared with the controls. Both peas and horse beans grew somewhat better in fresh distilled water than in distilled water in which pea seedlings had already been grown for 21 days.

Further preliminary experiments along this line gave similar results. Thus in another series, vigorous, thrifty plants of Canada field peas grown 10 days in full nutrient solution were transferred, after rinsing the roots, to distilled water, some being untreated and others treated. The treatment consisted in placing some of the cultures in an atmosphere of illuminating gas for 3 and 6 hours, and others in a gas-heated oven for 1 and 2 hours where it was not aimed to keep the temperature constant. For those cultures in the oven 1 hour the temperature at the outset was 53° C. and at the end 33° C., while for those remaining in the oven 2 hours the initial temperature was 60° C. and the final 33° C. The conductivity of the water was measured soon after the plants were placed in it but before the treatment, and again 5 days after treatment,

at which time the plants were discarded and a fresh lot of pea seedlings substituted.

The average reading (value of x) of the water for the 4 untreated controls at the beginning was 14.6 on the Wheatstone bridge, and with the same resistance in the box (9,110 ohms) it was 12.6 after 5 days. For the 4 cultures treated with illuminating gas (2 cultures for 3 hours and 2 cultures for 6 hours, the resultant effect being approximately the same for the two periods of exposure) the average initial reading was 17.0 for a resistance of 9,110 ohms, and at the end of 5 days it was 43.7 for a resistance of 1,000 ohms. In this case the increase in terms of specific conductivity was from 9.2×10^{-6} to 317.3×10^{-6}.

In the 4 cultures placed in the oven at the temperature designated there was no marked difference as regards variation in conductivity of the medium. The average initial reading was 17.2 and at the end (after 5 days) it was 12.4, the resistance in the box being 9,110 ohms in both readings. The rather high initial readings in the above cases are due to the fact that it was some hours after the roots were placed in the water before the readings were taken. In later work it was found to be advantageous to have the interval between placing the roots in the water and taking the first reading reduced to exactly one-half hour in order to obtain comparative data on the initial rate of exosmosis under different conditions.

We have, of course, no indication from the above regarding the exosmosis or conductivity curve during the 5-day interval. Subsequent work shows that it is very probable that the curve rose considerably in the case of the untreated and the oven-treated cultures and then fell, at the end of 5 days, to a position lower than that of the initial reading, due to the absorption being greater than the excretion after the first 2 or 3 days.

Let us turn now to the results obtained with the fresh seedlings grown in the same water in which the first crop had remained for 5 days under the conditions indicated above. After the second crop had been growing in this medium for just 15 days the green weight of tops of the 4 cultures in each group

was determined, with the following results, the figures representing the average green weight of tops in each culture:

Previous crop untreated	3.39 grams
Previous crop treated with illuminating gas	4.38 grams
Previous crop in oven 1 and 2 hrs. at 60–33°C	3.35 grams

V. Effects of Anesthetic Vapors

For this work the method used was to place the cultures (in some cases the medium also, in which instances the roots were in the water during exposure, and in other cases only the plants themselves, thus exposing the roots directly to the vapor) under bell jars into which the anesthetics were subsequently placed. In the case of ether and chloroform a meas-

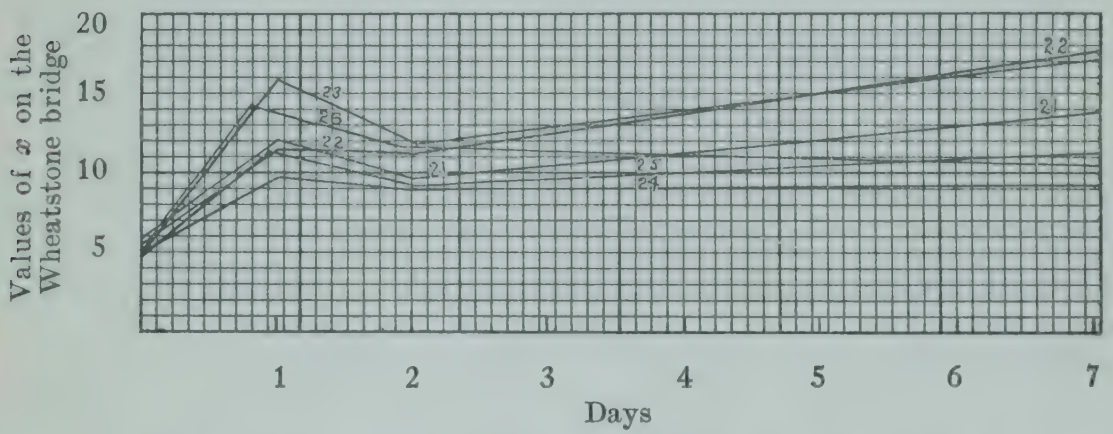

Fig. 1. Conductivity curves of cultures (series 11) in distilled water subsequent to treatment with anesthetics, as follows: No. 21, ether vapor, 1 minute, roots exposed; No. 22, control—roots exposed under bell jar 1 minute; No. 23, ether vapor, 2 minutes, roots exposed; No. 24, ether vapor, 5 minutes, roots exposed; No. 25, ether vapor, 10 minutes, roots exposed; No. 26, ether vapor, 15 minutes, roots exposed. The plants used were 39 days old. The first reading in each case is of the distilled water before the roots were placed in it.

ured amount of these agents was placed in an open evaporating dish under the bell jar, and after the treatment the residue was measured to determine the amount which had evaporated; in the case of the illuminating gas, however, the agent was run in until the air in the bell jar was more or less completely replaced. Where the plants alone were placed under the bell jars they were carefully attached by cheese-cloth bands to the leg of an inverted tripod, over which the bell jar was then placed.

In figures 1 and 2 are shown the results of treatment with ether and illuminating gas for varying periods of time. The plants for this experiment were 39 days old at time of treatment and had roots in good condition and well developed. The

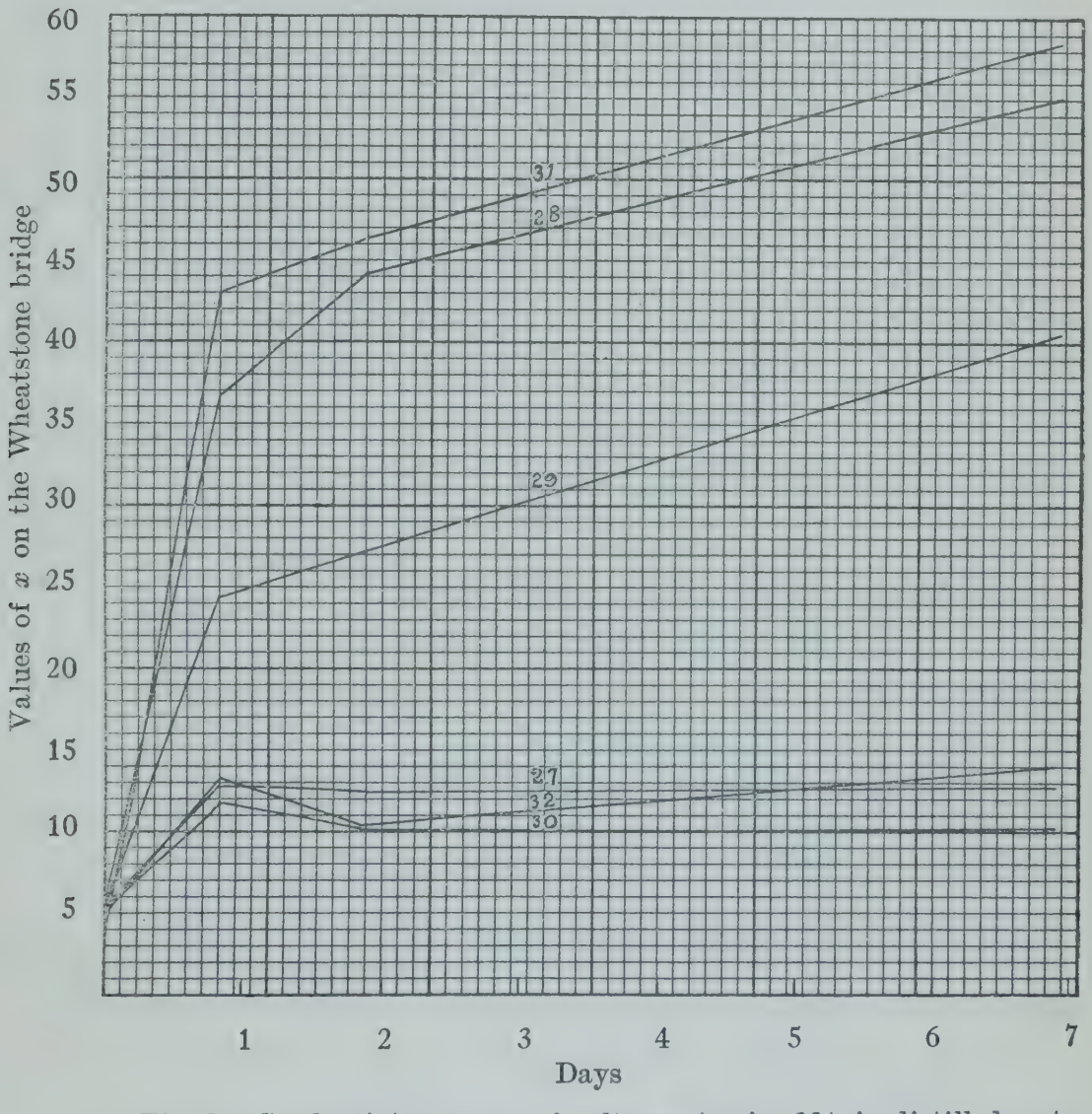

Fig. 2. Conductivity curves of cultures (series 11) in distilled water subsequent to treatment with anesthetics, as follows: No. 27, illuminating gas, 5 minutes, roots exposed; No. 28, illuminating gas, 10 minutes, roots exposed; No. 29, illuminating gas, 15 minutes, roots exposed; No. 30, control—roots exposed under bell jar 15 minutes; No. 31, ether vapor, 3 hours, roots in tumbler; No. 32, control—under bell jar 3 hours, roots in tumbler. The plants used were 39 days old. The first reading in each case is of the distilled water before the roots were placed in it.

first conductivity readings of the water were taken before the plant roots were introduced. As seen from the plotted results the ether had no effect on the exosmosis when the duration of the exposure ranged from 1 to 15 minutes; after 3

hours exposure, however, the exosmosis was pronounced, even when the roots were not in direct contact with the vapor.

An exposure of only 5 minutes to illuminating gas produced no effect, but one of 10 or 15 minutes' duration caused considerable exosmosis. That the 15-minute exposure should result in less exosmosis than the 10-minute one is an interesting point which finds an analogy, we shall see, at different places throughout the work, where in isolated cases a briefer exposure or milder treatment results in greater conductivity of the medium than a somewhat more prolonged exposure or more severe treatment. Where such a condition exists it is usually found near the boundary line of noticeable effect, and not where the effect is either nil or very pronounced. At this critical point the individual hardihood of the plants themselves seems the most plausible explanation of the difference. As the manipulation methods were exactly similar for any given series it is altogether unlikely that difference in technique was responsible for the variation.

The only plants to sustain any injury were those of cultures 28, 29, and 31. The tops of those in No. 31 drooped immediately after the treatment and soon died, though the leaves remained green; the roots, however, remained entirely normal to all appearances and retained their turgor. This is an interesting point and was referred to above. After 7 days Nos. 28 and 29 plainly showed some injury, but it was slight, and its visible effects were slow in making their appearance. At that time the tops of these cultures showed greater yellowing and drying than did those in the controls, No. 29 being somewhat more affected than No. 28; the roots of both, however, remained normal in appearance.

The greatest contrast between the treated plants and the controls is seen in fig. 3. The effect on the treated cultures corresponds to the duration of treatment, the curves especially showing the difference in the speed of initial exosmosis. It will be seen that the conductivity curves of the controls rise rather high during the first day. This is no doubt due to the effect of rather prolonged exposure of the roots to the air in the bell jar, even though it was saturated with water vapor.

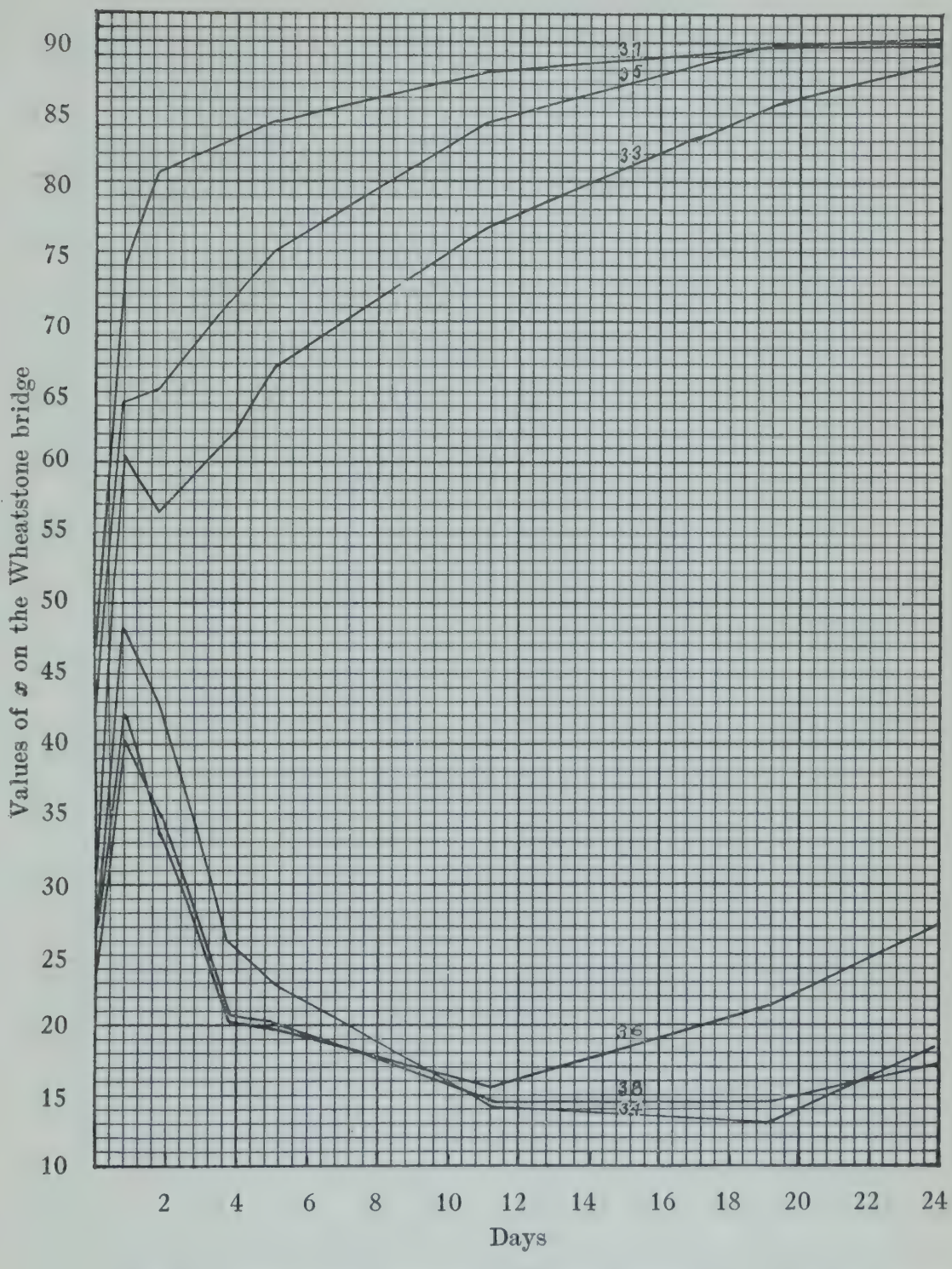

Fig. 3. Conductivity curves of cultures (series 11) in distilled water subsequent to treatment, as follows: No. 33, illuminating gas, 15 minutes, roots exposed; No. 34, control—roots exposed under bell jar 15 minutes; No. 35, illuminating gas, 30 minutes, roots exposed; No. 36, control—roots exposed under bell jar 30 minutes; No. 37, illuminating gas, 1 hour, roots exposed; No. 38, control—roots exposed under bell jar 1 hour. The plants were 22 days old when treated. The first readings were taken in the various cultures after the roots had been in distilled water for the following periods: No. 33, 35 minutes; No. 34, 1 hour and 15 minutes; No. 35, 1 hour and 13 minutes; No. 36, 1 hour and 25 minutes; No. 37, 1 hour and 5 minutes; No. 38, 1 hour and 16 minutes.

The subsequent decline in the curve, however, is characteristic for normal root tissues. It is also seen here that the 15-minute exposure to illuminating gas resulted in a greater rise in the conductivity curve than did a similar exposure in the case of the cultures recorded in fig. 2. That this is due to the different ages of the plants in the two cultures was borne out by treatment of plants of different ages with other agents. The older the tissues the more resistant they become to the toxic substance. McCool ('13) was the first to point this out, in his experiments with manganese chloride, and we see that it here holds for anesthetics as well.

Figure 4 shows the effect of illuminating gas at different intervals when only the tops are exposed directly to the gas, the roots meanwhile remaining in distilled water. The plants were affected in proportion to the duration of treatment. The tops of No. 39 were only very slightly injured, so that there was practically no difference between them and the tops of the controls; No. 41 was affected more; and No. 43 still more, finally dying, after progressive drooping and yellowing. But here again the roots of the treated plants were in all respects similar to those of the controls and entirely unaffected, visibly, even though exosmosis was considerable. In such cases it was also presumed that the excreted substances came in part from the tops and that here we had an illustration of the downward flow of food materials which occurs in plants under natural conditions. This presumption was considered experimentally as follows:

Some cultures were placed under a bell jar and treated with illuminating gas as before, the roots meanwhile being in distilled water. The tops of one culture were not cut off, while those of another were removed just before treatment, and finally those of a third were removed just after treatment. The controls were not treated, but their tops were cut off immediately after the roots were placed in the distilled water. The treated plants all gave approximately the same exosmosis, which was considerably more than that from the controls. A point to be noted here is that even though the treated tops which were not cut off were very much affected,

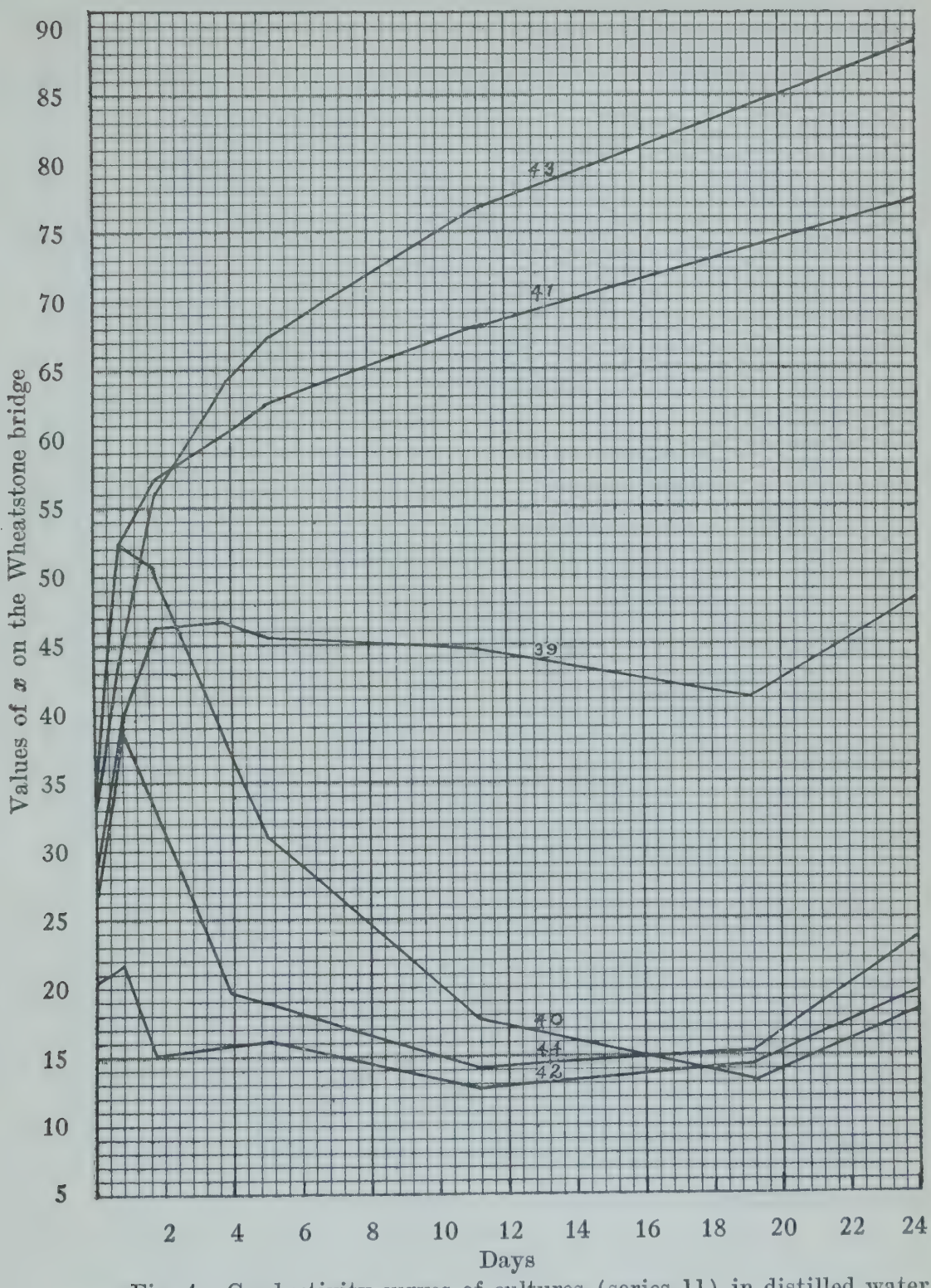

Fig. 4. Conductivity curves of cultures (series 11) in distilled water subsequent to treatment, as follows: No. 39, illuminating gas, 15 minutes, roots in tumbler; No. 40, control—under bell jar 15 minutes, roots in tumbler; No. 41, illuminating gas, 30 minutes, roots in tumbler; No. 42, control—under bell jar 30 minutes, roots in tumbler; No. 43, illuminating gas, 1 hour, roots in tumbler; No. 44, control—under bell jar 1 hour, roots in tumbler. The plants were 22 days old when treated. The first reading was taken in the various cultures after the roots had been in the distilled water subsequent to the treatment for the following periods (but to these periods should be added the time the cultures were under the bell jar, for the roots were in the distilled water during that interval also): No. 39, 2 hours and 12 minutes; No. 40, 2 hours and 23 minutes; No. 41, 2 hours and 20 minutes; No. 42, 2 hours and 30 minutes; No. 43, 2 hours and 11 minutes; No. 44, 2 hours and 23 minutes.

the roots meanwhile remaining practically normal, transpiration no doubt still continued. It remains an open question, however, whether such transpiration caused lower conductivity readings, due to the consequent absorption of electrolytes, than would have been the case had there been no, or only slight, transpiration, as in the cases where the tops were removed. The roots in all the cultures remained turgid and practically

TABLE II

EFFECTS OF ILLUMINATING GAS ON THE EXOSMOSIS FROM THE ROOTS OF PLANTS UNDER VARIOUS CONDITIONS

Culture no.	Treatment	Interval in dist. H_2O before first reading	Conductivity Readings*			
			After first interval	After 24 hrs.	After 88 hrs.	Increase‡ over dist. H_2O after 88 hrs.
1 and 2	Controls in dist. H_2O, no gas treatment. Tops cut off immediately after placing roots in dist. H_2O....	10 hrs.	33.6	37.9	41.8†	35.8†
3	Illuminating gas 1 hr.; roots in tumbler. Tops not cut off.....	1 hr., 17 min.	18.4	38.9	56.7	50.7
4	Illuminating gas 1 hr.; roots in tumbler. Tops cut off immediately after exposure.....	1 hr., 23 min	23.4	46.6	61.6	55.6
5	Illuminating gas 1 hr.; roots in tumbler. Tops cut off just before exposure.....	1 hr., 28 min.	18.6	41.2	60.5	54.5

* Readings represent the values of x on the Wheatstone bridge, resistance in box being 9,110 ohms.

† After 99 hours.

‡ The average reading of the distilled water before roots were placed in it was approximately 6.0.

normal. The higher readings of the treated cultures whose tops had been removed, over those of the untreated controls are to be considered as due to the effect of the illuminating gas, even though in one case only part of the plants was exposed to the agent. The results of this experiment are given in table II.

The results of ether vapor treatment for different periods are seen in fig. 5. An interesting point in this connection is the decline in the curves of the treated plants comparable in

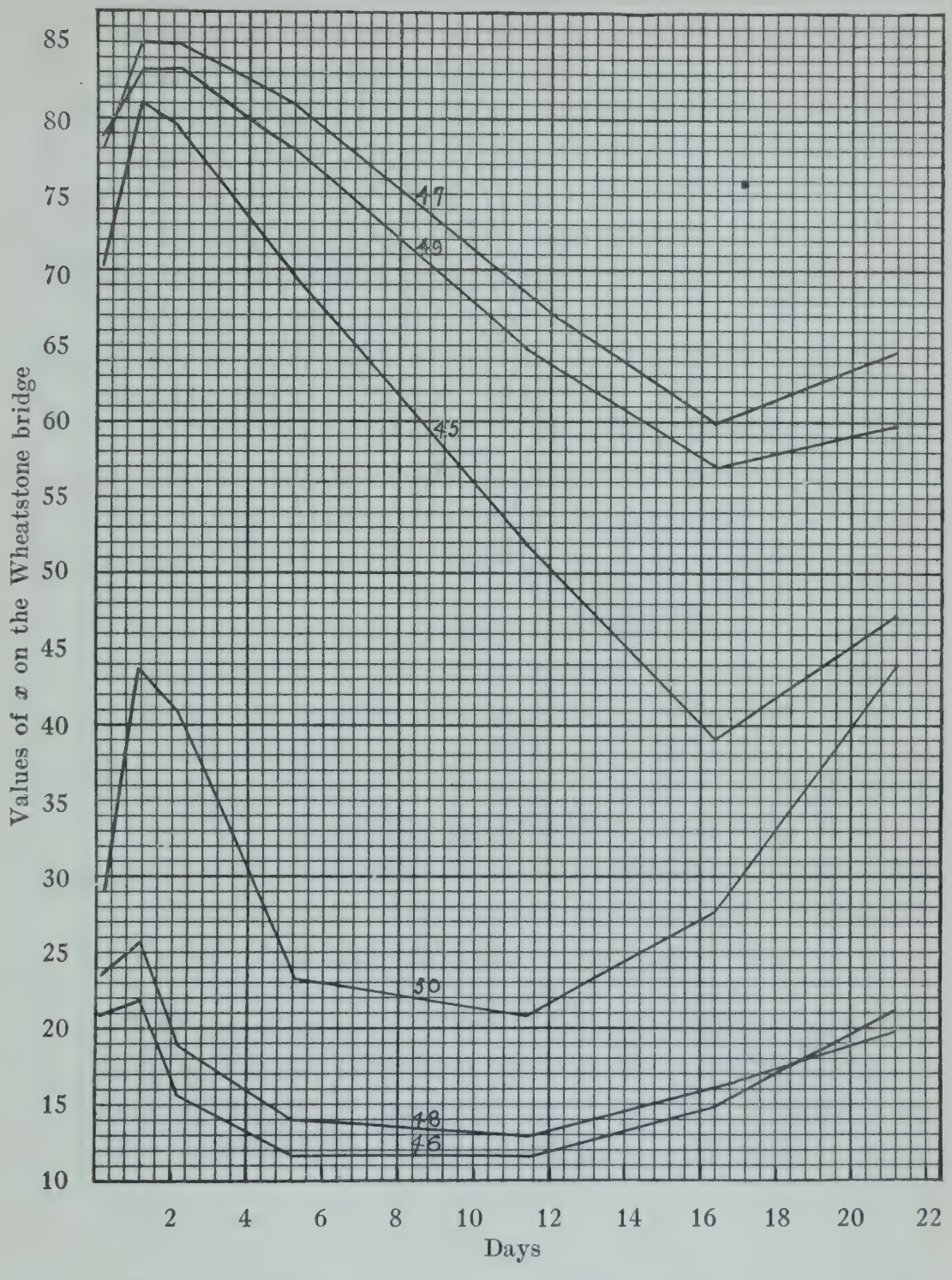

Fig. 5. Conductivity curves of cultures (series 11) in distilled water subsequent to treatment, as follows: No. 45, ether vapor, 30 minutes, roots exposed; No. 46, control—roots exposed under bell jar 30 minutes; No. 47, ether vapor, 1 hour, roots exposed; No. 48, control—roots exposed under bell jar 1 hour; No. 49, ether vapor, 2 hours, roots exposed; No. 50, control—roots exposed under bell jar 2 hours. The plants were 25 days old at the time of treatment. In culture 49, 17cc. of the initial 50cc. of ether remained at the end of the 2 hours. The first reading plotted in each case was taken after the roots had been in the distilled water subsequent to the treatment for the following periods: No. 45, 1 hour and 1 minute; No. 46, 1 hour and 12 minutes; No. 47, 1 hour and 27 minutes; No. 48, 1 hour and 38 minutes; No. 49, 1 hour and 17 minutes; No. 50, 1 hour and 28 minutes.

some respects to that in the curves obtained from normal plants. A distinction should be made here, however, from the causal agency in this decline in conductivity and the anesthetic reversibility that Osterhout ('13) describes. The decline in the curve indicates that the absorption of electrolytes by roots occurs at a greater rate than they are excreted, for both processes, absorption and excretion, are undoubtedly going on and the curve represents the proportionate amounts of each for any given time. Thus if A represents the excretion and B represents the absorption, the curve declines when B is greater than A, and inclines when A is greater than B. Hence the curve may be represented as $A - B = C$, where C represents the number of ions or charge-carriers in the solution. The tops of the treated plants showed no visible effects whatever when compared with the controls. The roots of No. 45 were very slightly affected, but those of Nos. 47 and 49 were considerably so and to about an equal degree, as shown by flaccidity, root coloration, and the colored and turbid appearance of the medium; the tops, however, continued normal for 21 days after the treatment. Hence the metabolic processes no doubt proceeded unimpaired in many respects, as did also transpiration. The decline of the conductivity curve therefore represents merely a partial return to normal conditions. But the higher conductivity of the medium shows greater exosmosis than from the normal plants. This is due to the unalterable and invariable (and not reversible) effect of the anesthetic upon certain cells. Culture 50 shows in the higher position of its curve, as compared with the other controls, an effect that is no doubt due to the 2-hour exposure of the roots to the air in the bell jar.

As seen in fig. 6 no marked results followed the ether application for one-half to two hours when the roots were in the water during the treatment, though a slight rise is evident for the culture exposed 2 hours. No visible effects were produced on either the tops or roots.

Comparing the effects on plants of an ether vapor-saturated atmosphere with those produced by an illuminating gas-saturated atmosphere, it is thus seen that illuminating gas is much

more injurious than is ether vapor under the conditions of the experiment. Equal amounts of each might give different results, however. The gas used was a mixture of water- and coal-gas with a specific gravity of .62 as compared with air;

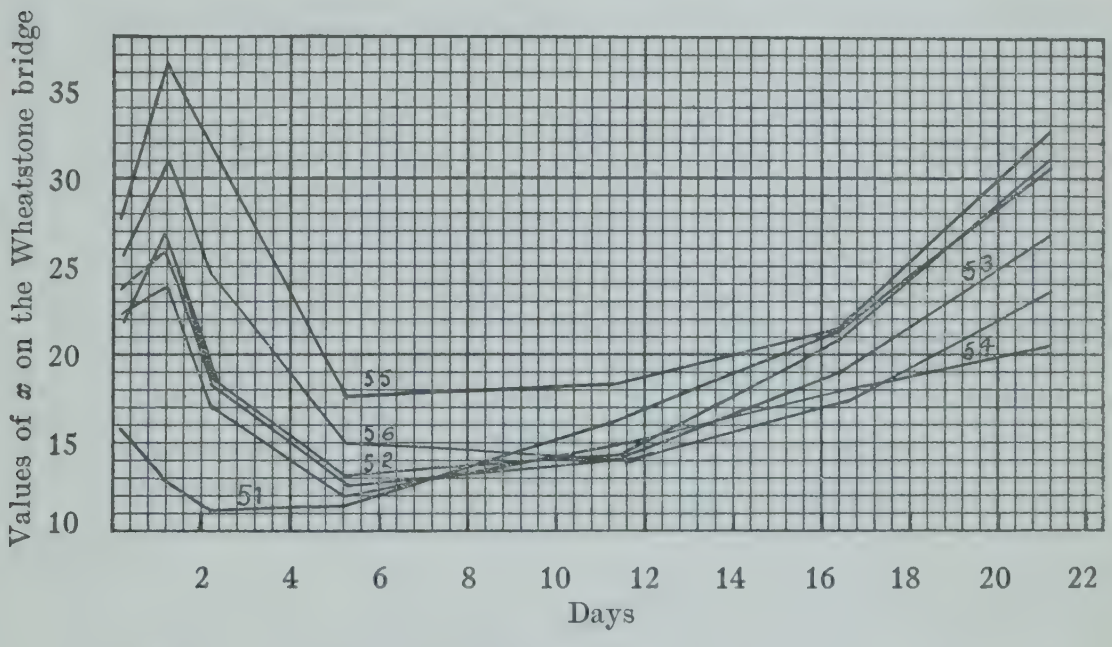

Fig. 6. Conductivity curves of cultures (series 11) in distilled water subsequent to treatment, as follows: No. 51, ether vapor, 30 minutes, roots in tumbler; No. 52, control—under bell jar 30 minutes, roots in tumbler; No. 53, ether vapor, 1 hour, roots in tumbler; No. 54, control—under bell jar 1 hour, roots in tumbler; No. 55, ether vapor, 2 hours, roots in tumbler; No. 56, control—under bell jar 2 hours, roots in tumbler. The plants were 25 days old at the time of treatment. In culture 55, 60cc. of the initial 100cc. of ether remained at the end of the 2 hours. The following periods represent the time elapsing in the various cultures between the removal of the cultures from the bell jar and the taking of the first reading (to which period should be added the duration of treatment, for the roots were in the distilled water during that time also): No. 51, 1 hour and 24 minutes; No. 52, 1 hour and 46 minutes; No. 53, 1 hour and 51 minutes; No. 54, 2 hours and 6 minutes; No. 55, 1 hour and 39 minutes; No. 56, 1 hour and 50 minutes.

one of the daily samples analyzed by the gas company (the officials of which kindly supplied the writer with the data and informed him that they may be considered an approximately fair average) showed the following constituents:

CO_2	3.0%
O_2	.5%
Illuminants (unsaturated hydrocarbons, e. g., ethylene and acetylene)	7.0%
CO	16.1%
CH_4	25.6%
H_2	42.8%
N_2	5.0%

Crocker and Knight ('08), in their work on the question of injury by illuminating gas and its constituents, concluded that "there is much evidence that indicates that the toxic limits of illuminating gas upon these flowers [carnations] is determined by the ethylene it contains." They used a small greenhouse of 1.69 cubic meters' capacity in which they placed potted plants for varying intervals, specified amounts of gas being introduced. The buds were easily injured but the vegetation was apparently not affected even after an exposure of about 72 hours, during which 10 liters of gas had been introduced, 2 or 4 liters at a time. The method was therefore somewhat different from the one employed by the author, in which the plants were placed in an atmosphere saturated with illuminating gas, but for a much shorter period. The underlying cause of the effect in both cases, however, is probably the same.

The etherization of plants as a practical process has been in operation for many decades, especially as a means of hastening the activities of plants, particularly of bringing them into bloom earlier. Some experimental work has also been done, as we have seen, on the effect of such treatment (though in most cases only when the anesthetics were in solution) upon the exosmosis of non-electrolytes, as determined by various methods, from plant or animal cells. It is interesting, therefore, to observe the exosmotic phenomena of electrolytes when the plants are anesthetized under various conditions.

To determine whether the amount of substance excreted corresponded to the conductivity readings, the water in the tumblers was evaporated and the residue weighed. The following are the results:

Total wt. of substance from illuminating gas-treated cultures (Nos. 33, 35, 37, 39, 41, and 43)	0.1514 grams
Total wt. of substance from ether-treated cultures (Nos. 45, 47, 49, 51, 53, and 55)	0.0674 grams
Total wt. of substance from the 12 controls	0.1077 grams
Total wt. of substance from 6 controls, therefore	0.0538 grams

We may obtain a rough basis for estimating this residue in terms of NaCl by comparing the figures just given with the data on a previous page which gave the corresponding specific conductivity values for some values of x on the Wheat-

stone bridge and also for various concentrations of NaCl. Thus 0.15 gram residue was obtained from 1500 cc. of the media from illuminating gas-treated cultures. This is equivalent to 0.10 gram in 1 liter, which in terms of NaCl would be

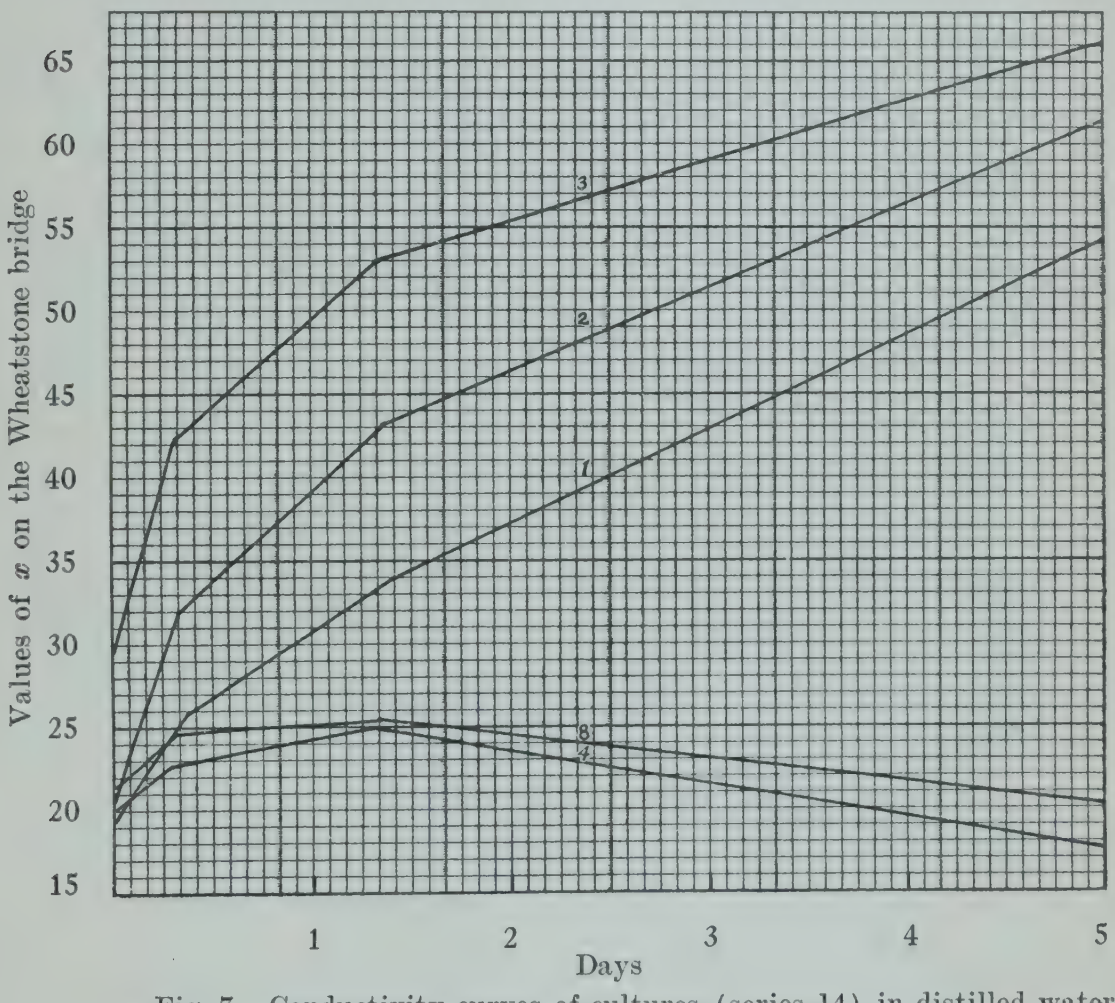

Fig. 7. Conductivity curves of cultures (series 14) in distilled water subsequent to treatment, as follows: No. 1, temperature of —6 to —2°C., 1 hour, roots in tumbler; No. 2, temperature of —6 to —2°C., 2 hours, roots in tumbler; No. 3, temperature of —6 to —2°C., 3 hours, roots in tumbler; No. 4, control—room temperature, roots in tumbler; No. 8, control—room temperature, roots in tumbler. The plants were 23 days old at the time of treatment. The first reading was taken in each case after the roots had been in the distilled water for the following respective periods (cultures 1–3 were being treated during part of that time): No. 1, 1 hour and 47 minutes; No. 2, 2 hours and 29 minutes; No. 3, 3 hours and 45 minutes; No. 4, 3 hours and 6 minutes; No. 8, 2 hours and 2 minutes.

approximately N/500. The specific conductivity of N/500 NaCl is about 25×10^{-5}, the x value of which on the Wheatstone bridge is 85. The average final reading of the 6 cultures treated with illuminating gas is 79.5. Hence the residue in terms of NaCl would be in the neighborhood of N/500.

VI. Effects of High and Low Temperatures

After the preliminary experiments noted above on the effect of heat had been carried out it was desired to study the question further and determine the resulting exosmosis curves at the extreme temperatures, high and low. The preliminary experiments had involved temperatures requiring a considerable time interval to produce positive results. The data now to be presented concern temperatures sufficient in themselves to effect decided injury in a very short period. By varying the time factor, therefore, results could readily be obtained on both sides of the point of injury.

For the experiment, the results of which are plotted in fig. 7, cultures were set out of doors for the time indicated, directly exposed to the winter temperature. The tops showed some signs of freezing after a few moments, but the effects did not become noticeably worse until the cultures were brought inside, when all the plants in each culture immediately drooped over the wire supports and became entirely limp, and soon died. The tops did not yellow, but retained the green color after death. Except for the root tips of the plants in No. 3, which were slightly brown at the end of 5 days, all the roots of the treated plants remained turgid, white, normal, and in healthy condition. This is interesting in view of the fact that while no ice was formed in No. 1, there was a slight fringe of it between the water and the tumbler in No. 2, and a hollow cylinder of ice one-fourth inch thick formed next to the tumbler wall in No. 3. In the last-mentioned culture there was also a film of ice over the surface of the water and the roots were frozen to the ice mass so that on lifting the plants from the tumbler the mass of ice adhered to the roots. The first readings were taken only after the ice had melted. The temperature at first was —6° C. but by the end of the first hour it had risen to —2° C., where it remained practically constant for the balance of the interval.

At a temperature of —6.5° C. it is seen by reference to fig. 8 that while for exposures of the plants alone (the roots being out of the water) of 2 and 3 minutes, marked exosmosis imme-

diately results, exposures of 1 minute or $\frac{1}{2}$ minute produce no results. Culture 13 has rather high exosmosis for a control,

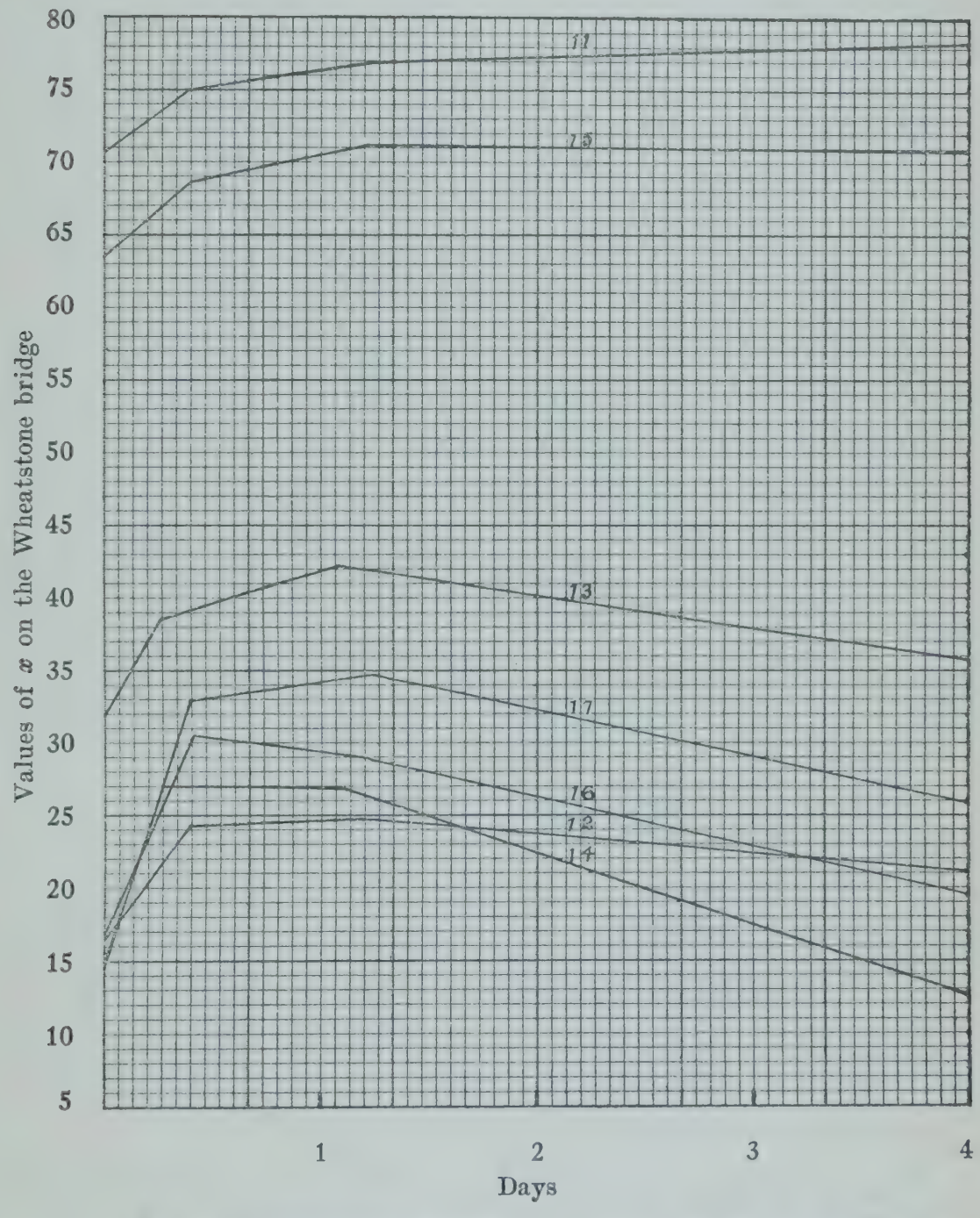

Fig. 8. Conductivity curves of cultures (series 14) in distilled water subsequent to treatment, as follows: No. 11, temperature of — 6.5°C., 3 minutes, roots exposed; No. 12, control—roots exposed to laboratory temperature 15 minutes; No. 13, control—roots exposed to laboratory temperature 30 minutes; No. 14, control—roots exposed to laboratory temperature 5 minutes; No. 15, temperature of — 6.5°C., 2 minutes, roots exposed; No. 16, temperature of —6.5°C., 1 minute, roots exposed; No. 17, temperature of —6.5°C., one-half minute, roots exposed. The plants were 24 days old at the time of treatment. The first reading was taken in each case after the roots had been in the distilled water for exactly 30 minutes subsequent to the treatment.

but this is readily accounted for by the exposure of its roots to the atmosphere of the laboratory for 30 minutes, a condition noted in other cases above.

Cultures 9 and 10 of this series, the results from which are not represented because both tops and roots were killed outright, the resulting exosmosis therefore being immediate and high (x being about 88.0 cm.), were exposed for 15 and 33 minutes respectively to a temperature of — 6.5°C., the roots being out of the medium. In a very short time, on returning them to the laboratory, the tops wilted and drooped over the supporting wires and the roots became very flaccid. In the case of No. 11, however, an interesting gradation or intermediate condition was observed between it and Nos. 9 and 10 on one hand and between it and the controls on the other. While the tops in No. 11 wilted and drooped somewhat soon after being returned to the higher temperature of the laboratory, they did not become entirely limp and the roots were only slightly less turgid than those of the controls. Even after 4 days the tops of No. 11 were not drooping much, though the tips of the branches and the upper leaves were dead; the lower part of the stems and the lower leaves remained green and normal. The lateral roots and the older part of the main roots remained nearly normal, but the tips of the latter were flaccid and shrunken for about 2 inches. Culture 15 showed a very slight flaccidity in the tops and roots soon after the treatment, and after 4 days some of the younger leaves and the tips of the older leaves were blackened, curled, and dried somewhat, but the great part of the tops remained normal in appearance; the roots were slightly flaccid at the tips, but were in general practically normal. Cultures 12, 13, 14, 16 and 17 were normal in respect to both roots and tops.

The interval between 15 and 30 minutes is shown in fig. 9 to be the critical period for the pea plants exposed in a tumbler to a temperature of from — 2°C. to — 2.5°C., for an exposure of 30 minutes caused considerable exosmosis, while one of 15 minutes gave a curve approximately that for normal plants.

To contrast the effects of low and high temperatures, Nos.

25–28 inclusive are plotted in the same figure with Nos. 18 and 23. With plants enveloped in a steam bath the injury, as expected, is very speedy and effective. Even one-half minute —when the roots are exposed—causes immediate and marked

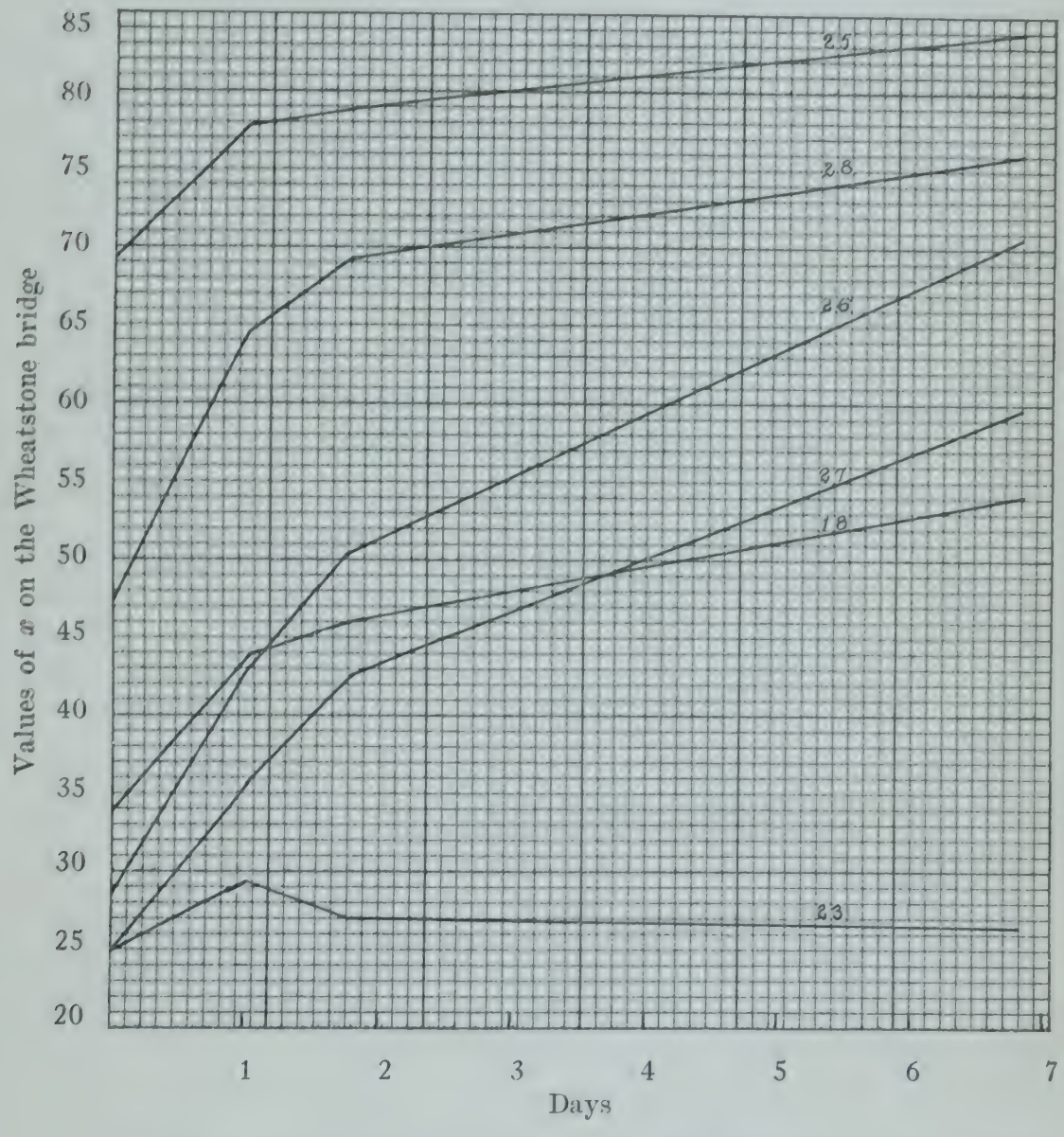

Fig. 9. Conductivity curves of cultures (series 14) in distilled water subsequent to treatment, as follows: No. 18, temperature of —2.5°C., 30 minutes, roots in tumbler; No. 23, temperature of —2.0°C., 15 minutes, roots in tumbler; No. 25, steam, one-half minute, roots exposed; No. 26, steam, 2 minutes, roots in tumbler; No. 27, steam, 1 minute, roots in tumbler; No. 28, steam, 10 minutes, roots in tumbler. The plants were 29 days old at the time of treatment. The first reading was taken in each case after the roots had been in the distilled water for the following respective periods (the cultures whose roots were in tumblers during the treatment were likewise in the distilled water): No. 18, 4 hours and 49 minutes; No. 23, 4 hours and 41 minutes; No. 25, 4 hours and 43 minutes; No. 26, 4 hours and 29 minutes; No. 27, 4 hours and 31 minutes; No. 28, 4 hours and 12 minutes.

exosmosis which is greater than that caused by a 10-minute exposure when the roots are in distilled water meanwhile. The condition of the plants immediately after the treatment and again after 7 days is given in table III. Here again is illus-

TABLE III

CONDITION OF PLANTS AFTER EXPOSURE TO VARIOUS TEMPERATURES

Culture no.	Condition of tops	Condition of roots
	Condition of plants immediately after the treatment:	
18	Considerably flaccid and drooping	Entirely normal
23	Very slightly drooping, nearly normal	Entirely normal
25	Drooping considerably	Normal
26 and 27	Drooping, green and damp	Normal
28	Drooping, green and damp	Apparently practically normal
	Condition of plants 7 days after the treatment:	
18	About half dead and half alive; 3 live stems with green, normal leaves	Entirely normal
23	Almost normal; tips of a few stems killed and some slightly injured, but some stems normal throughout; a few blackened leaves, but for the most part stems and leaves green and normal	Entirely normal
25	Dead	Only very slightly flaccid and nearly normal in appearance
26 and 27	Dead	Practically normal in appearance
28	Dead	Almost normal

trated, therefore, the case where there is considerable exosmosis without very marked visible effects resulting to the root tissues.

The effects of moist heat, as graphically represented in fig. 9, having been considered, we may now turn our attention to fig. 10, where the results are plotted of an exposure of plants to dry heat for short intervals, both with the roots directly exposed and with the roots remaining in the tumbler of water during the treatment.

It is seen that definite and positive exosmosis is obtained after a 4-minute exposure of the unprotected roots. The decline of the curve of No. 29, roots exposed for 2 minutes, is probably best accounted for by assuming greater hardihood of the plants in that culture, or that some condition effected an increase in transpiration. A 1-minute exposure (No. 30) pro-

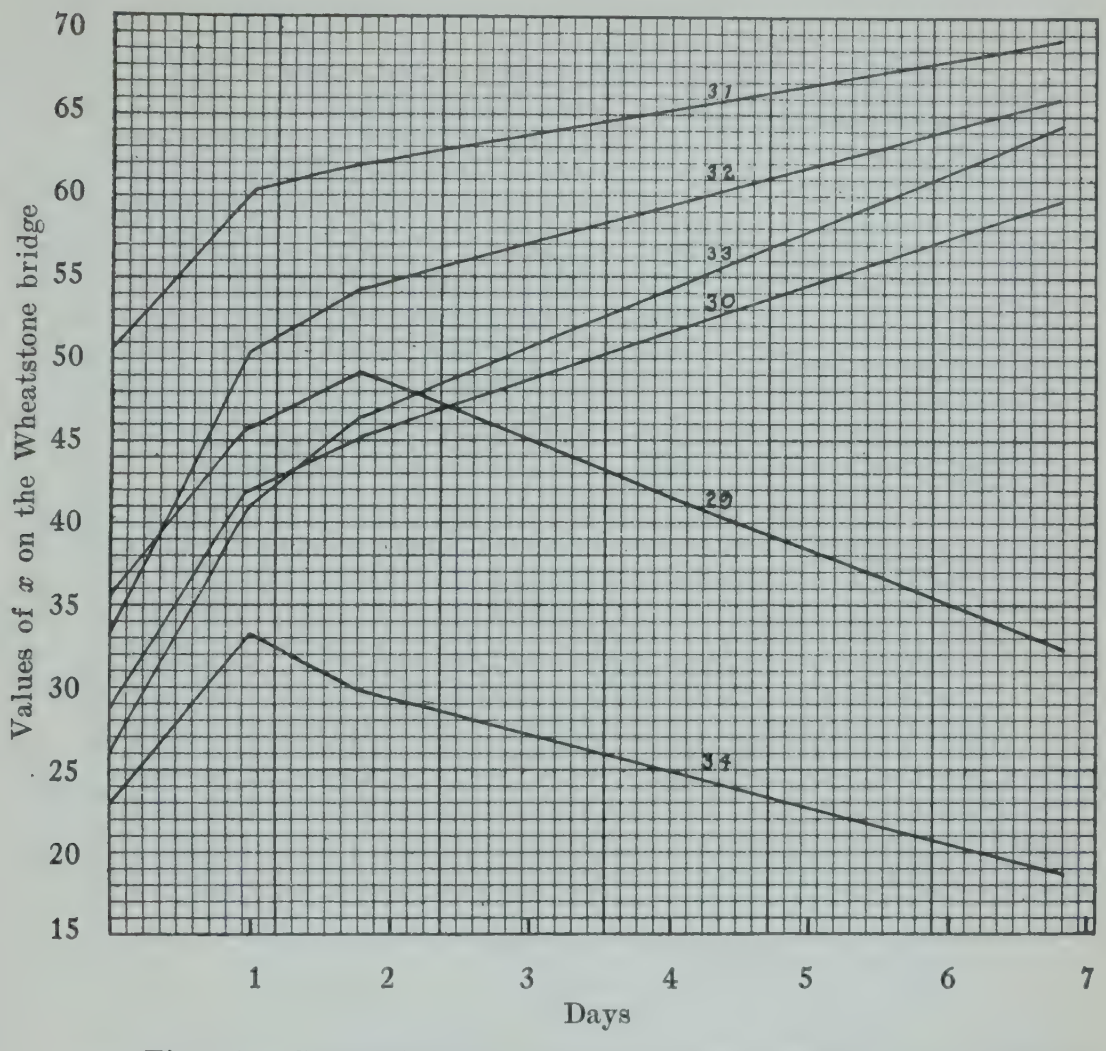

Fig. 10. Conductivity curves of cultures (series 14) in distilled water subsequent to treatment, as follows: No. 29, temperature of 92°C., 2 minutes, roots exposed; No. 30, temperature of 92°C., 1 minute, roots exposed; No. 31, temperature of 92°C., 4 minutes, roots exposed; No. 32, temperature of 92°C., 2 minutes, roots in tumbler; No. 33, temperature of 92°C., 4 minutes, roots in tumbler; No. 34, control—roots in tumbler at laboratory temperature. The plants were 29 days old at the time of treatment. The first reading was taken in each case after the roots had been in the distilled water for the following respective periods (the cultures whose roots were in tumblers during the treatment were likewise in the distilled water during that time): No. 29, 2 hours and 47 minutes; No. 30, 2 hours and 48 minutes; No. 31, 2 hours and 44 minutes; No. 32, 2 hours and 45 minutes; No. 33, 2 hours and 46 minutes; No. 34, 2 hours and 46 minutes.

duced less exosmosis at the beginning than was the case in No. 29, but finally caused more. The same irregularity is also noticed in Nos. 32 and 33. These irregularities near the boundary line of endurance have been discussed above. The tops of Nos. 29–33 were killed by the treatment, but the roots of all remained practically normal in appearance except in No.

31, where the tips were slightly shrunken at first but became almost normal in the water after 7 days.

In the temperature experiments we have thus used the extremes of temperature and have reduced the interval of exposure in order to approach the point at which the effect is just evident.

VII. Effects of Anesthetics in Solution

Having seen some of the effects of anesthetic vapors, we may turn our attention next to the results obtained with anesthetics in solution. In the investigations of others pertaining to the effect of anesthetics, already cited, the result has been almost universally noted that small amounts of anesthetics decrease the exosmosis of coloring matters, etc., while toxic amounts increase it. In most cases this exosmosis was explained on the basis of an alteration in the plasma membrane, small amounts of the anesthetics presumably reducing the permeability and large amounts increasing it. But a point worthy of note is that wherever such effects have been determined the substance under observation was either a colored compound or one of complex organic nature.

Thus Czapek ('11) used the myelin-formation of a tannoid substance, anthocyan, as a basis of observation. From the standpoint of a physical phenomenon, i. e., the lowering of surface tension, his experiments beautifully illustrated the principle under consideration. But from the standpoint of exosmosis in the broader sense we must include electrolytes (salts, bases, and acids) as well as tannin compounds in any discussion dealing with agents affecting exosmosis, and while the critical concentrations which he determined are undoubtedly characteristic of the plants and the compounds studied, the results given herewith show that they are not the limiting concentrations which effect the exosmosis of electrolytes from the roots of certain plants. The limiting concentrations which he found are given in table IV.

Czapek believed the permeability of the plasma membrane was altered under the influence of alcohols, ethers, etc., so that abnormal exosmosis occurred. Whatever may be the expla-

TABLE IV

CRITICAL CONCENTRATIONS (THOSE JUST SUFFICIENT TO CAUSE EXOSMOSIS) OF SOME ORGANIC COMPOUNDS AS DETERMINED BY CZAPEK FOR CERTAIN PLANTS

Agent	Plant	Concentration of agent	Surface tension*
Methyl alcohol	*Echeveria*.....	18% aqueous solution (by volume)	.71
Ethyl alcohol	*Echeveria* and *Saxifraga*	10–13% aqueous solution (by volume).....	.65–.70
Ethyl ether	*Echeveria* and *Viola*	$\frac{1}{4}$–$\frac{1}{2}$ saturated aqueous solution acting for 24 hrs...	.61–.71
Chloroform	*Echeveria*..	Saturated aqueous solution†.... ..	.98
Chloral hydrate	.....	3.09% aqueous solution.....	.93
Ethyl acetate	Saxifraga hairs and variegated leaves of *Oplismenus imbecillus*	3% aqueous solution acting for 12 hrs..	.69–.73
Ethyl acetate	Red beets.....	2% aqueous solution acting for 12 hrs..	

* In terms of water as unity. † After 24 hours the cells had lost all tannin.

nation for the phenomena observed, it will be seen by comparing the results in the following experiments with the data just given that the limiting values found for the exosmosis of electrolytes do not at all correspond to the values found by Czapek for the exosmosis of the tannoid substance.

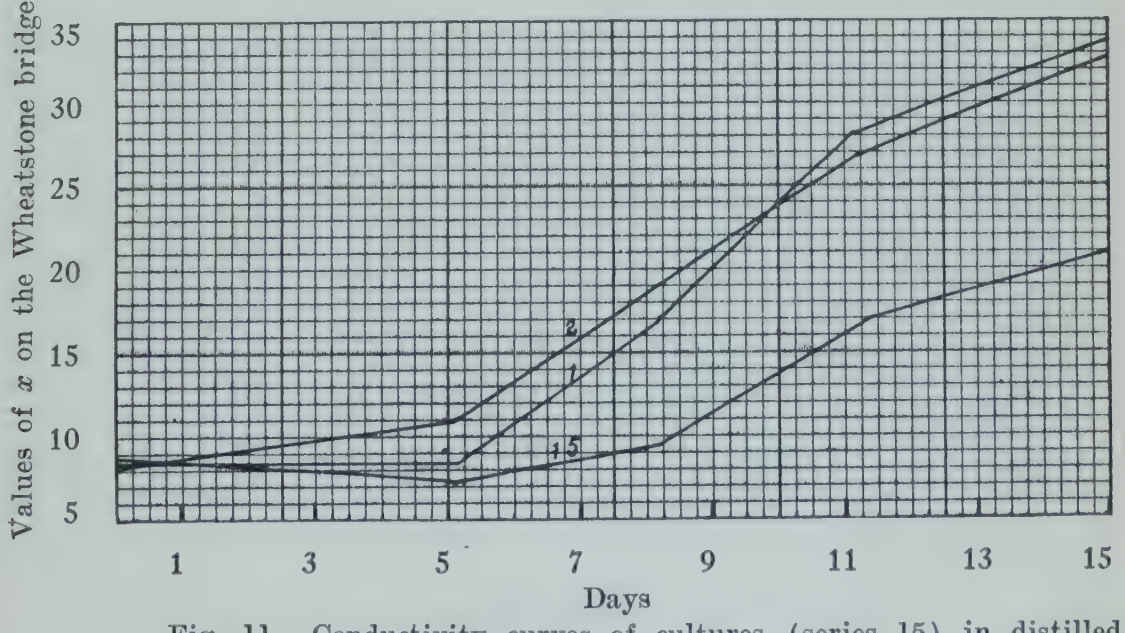

Fig. 11. Conductivity curves of cultures (series 15) in distilled water subsequent to treatment, as follows: No. 1, ether vapor, 15 minutes, roots exposed; No. 2, 1 per cent ether in water, 15 minutes; No. 15, control—roots exposed under bell jar 15 minutes. The plants were 31 days old when treated. In culture 1, 11cc. of the initial 15cc. of ether remained after the 15-minute exposure. In Nos. 1 and 2, the first reading was taken exactly 30 minutes, and in No. 15, 48 minutes, after the roots were placed in the distilled water.

In fig. 11 are shown the results with ether in distilled water and, for comparison, also with ether vapor for the same period. The curves for the ether-treated cultures are closely parallel for the entire period of observation of 15 days, and both are

TABLE V

EFFECTS OF VARIOUS ANESTHETICS ON THE EXOSMOSIS FROM THE ROOTS OF PLANTS

(See curves in fig. 12)

Anesthetic	Time of exposure	Culture no.	Resulting exosmosis
Vapor Treatment, Roots Exposed			
Ether	30 minutes	3	About the same in Nos. 3 and 5
Illuminating gas	15 minutes	5	
Illuminating gas	30 minutes	7	Higher
Chloroform	30 minutes	9	Highest
Treatment with Anesthetics Dissolved in Water			
Ether, 4%	30 minutes	4	High
Ether, 4%	Throughout experiment	11	Highest
Ether, 10%	30 minutes	12	Higher
Illuminating gas-saturated sol'n.	15 minutes	6	Medium low
Illuminating gas-saturated sol'n.	30 minutes	8	Like control
Illuminating gas-saturated sol'n.	Throughout experiment	13	Medium low
Illuminating gas-saturated sol'n. frequently re-saturated	30 minutes	14	Slightly above control
Chloroform, 4%	30 minutes	10	Very high
Controls			
Roots exposed to the air under a bell jar 30 minutes		16	High for control
Roots exposed to the air under a bell jar 30 minutes		17	High for control
Roots not exposed, but in water from first		18	Normal for control

above that of the control. The excretion was nil during the first half hour and at the end of 5 days it was scarcely more, though it may have risen and fallen in the meantime, as no readings were taken in the interim. After 5 days a greater rise in the conductivity curve occurred with the ether-treated cultures than with the control; no apparent effects, however, were produced on either the tops or roots.

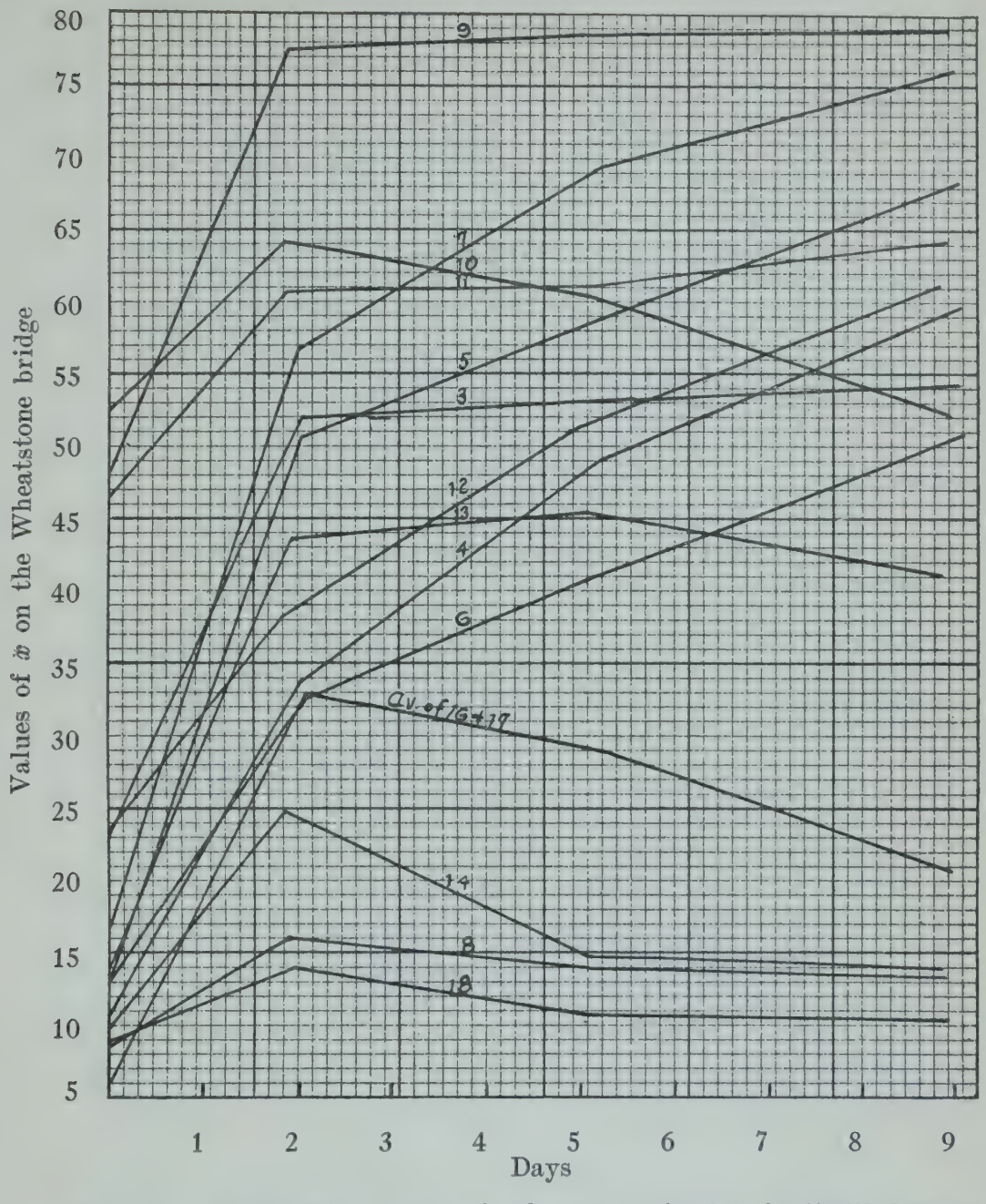

Fig. 12. Conductivity curves of cultures (series 15) in distilled water subsequent to treatment, as follows: No. 3, ether vapor, 30 minutes, roots exposed; No. 4, 4 per cent ether in water, 30 minutes; No. 5, illuminating gas, 15 minutes, roots exposed; No. 6, distilled water saturated with illuminating gas, 15 minutes; No. 7, illuminating gas, 30 minutes, roots exposed; No. 8, distilled water saturated with illuminating gas, 30 minutes; No. 9, chloroform vapor, 30 minutes, roots exposed; No. 10, 4 per cent chloroform in water, 30 minutes; No. 11, 4 per cent ether in water, to the end of the experiment; No. 12, 10 per cent ether in water, 30 minutes; No. 13, distilled water saturated with illuminating gas, to end of experiment; No. 14, distilled water saturated with illuminating gas, 30 minutes (frequently saturated); No. 16, control—roots exposed 30 minutes under bell jar; No. 17, control—roots exposed 30 minutes under bell jar; No. 18, control—roots placed directly into distilled water. The percentages given above refer to volume-per cent. The plants were 37 days old when treated. The first reading was made after the roots had been in distilled water 30 minutes (No. 10, 36 minutes). In all cases treatment preceded placing of the roots in distilled water (conductivity of which was determined except in the cases of Nos. 11, 13, and 18). In culture 3, 17cc. of the initial 25cc. of ether remained at the end of the 30-minute exposure; in culture 9, 23.5cc. of the initial 25cc. of chloroform remained.

To show the comparative effects on the exosmosis from the roots of plants treated with ether, chloroform, and illuminating gas—both when applied as vapor and when introduced into the water—the conductivity curves of fig. 12 were plotted. The results, somewhat classified, are also given in table v. It will be seen that the quantity of anesthetics used and the duration of treatment varied in individual cases.

The indications are, therefore, that for an equal exposure the vapors range in order of effectiveness as follows: ether, least; illuminating gas, more; and chloroform, most. The difference in effectiveness between the ether and the chloroform is especially interesting, more so when we note that 8 cc. of ether were used and only 1½ cc. of chloroform. This would seem to be in harmony with the findings of Graham ('14); he was able to produce liver necrosis by some aliphatic halogen substituted compounds, but not by ether or chloral hydrate.

As regards the fact that No. 11 (4 per cent ether, remaining in the water) has a higher curve than No. 12 (10 per cent ether for 30 minutes) and especially at the beginning, it should be stated that in the case of Nos. 4, 6, 8, 10, 12, and 14, the treatment was given while the roots were in distilled water plus the anesthetics. Following the treatment the roots, after rinsing, were placed in distilled water, and at the end of one-half hour the first reading was taken. In the case of Nos. 11 and 13 the water containing the anesthetic was not replaced by fresh water and the first reading was taken one-half hour after the treatment began. Since the exosmosis during the first half hour is unusually rapid as a result of anesthetic treatment, it will be seen that in replacing the medium at the end of that period, the excreted material was thus discarded for that interval. Hence, such curves represent a secondary exosmosis. The curve of No. 11, therefore, is for total exosmosis, while that of No. 12 is for partial exosmosis.

The condition of the cultures which furnished the results plotted in fig. 11 is given for various periods in table vi.

In fig. 13 the secondary exosmosis after the first half hour is graphically represented for some organic compounds in considerable concentration. The purpose was, of course, to use a

concentration sufficiently effective to give results in a short interval of time. After the treatment the roots were rinsed and placed in distilled water. It is interesting to note that the alcohols used were only slowly effective at first, but that

TABLE VI

CONDITION OF PLANTS AFTER TREATMENT WITH ANESTHETICS

Culture no.	Condition of tops	Condition of roots
Condition of plants 2 days after treatment:		
3 and 4	Slightly subnormal, but almost normal	Somewhat flaccid
5	Practically same as in Nos. 3 and 4	Practically normal
6	Practically same as in Nos. 3 and 4	Practically normal, but somewhat flaccid
7	Practically all dead	Somewhat flaccid
8	Almost normal	Slightly flaccid
9, 10, 11, and 12	Normal	Considerably flaccid
13	Normal	Practically normal
14	Normal	Slightly flaccid
16, 17, and 18	Normal	Normal
Condition of plants 9 days after treatment:		
3	Much dried and yellowed	Practically normal
4	Slightly worse than in No. 3	Considerably flaccid
5	Same as in No. 4	Less flaccid than in No. 4
6	Mostly dried up	Practically normal
7	All dried up	Slightly flaccid
8	Practically normal	Practically normal
9	Practically normal	Considerably flaccid
10	Practically normal	Somewhat flaccid
11 and 12	Almost normal	Somewhat flaccid
13 and 14	Normal	Practically normal
16	Slightly subnormal	Practically normal
17 and 18	Normal	Normal

after 8 days the conductivity readings for those cultures were as high as those of the other cultures. Benzol and toluene produced almost identical effects. The effect produced by chloral hydrate remained constant after 1 day. Ethyl acetate and benzaldehyde were especially effective. The condition of the plants at the end of 8 days is given in table VII.

In fig. 14 are shown the effects of smaller amounts of the same substances, the curves of which are exhibited in fig. 13. Here, however, concentrations only one-fourth as great as those previously employed were used, but the chemicals were allowed to remain in the water during the entire period (or until evaporated, as may have been the case with some).

While the alcohols gave a greater effect than the control, they gave no greater exosmosis than one of the controls in the

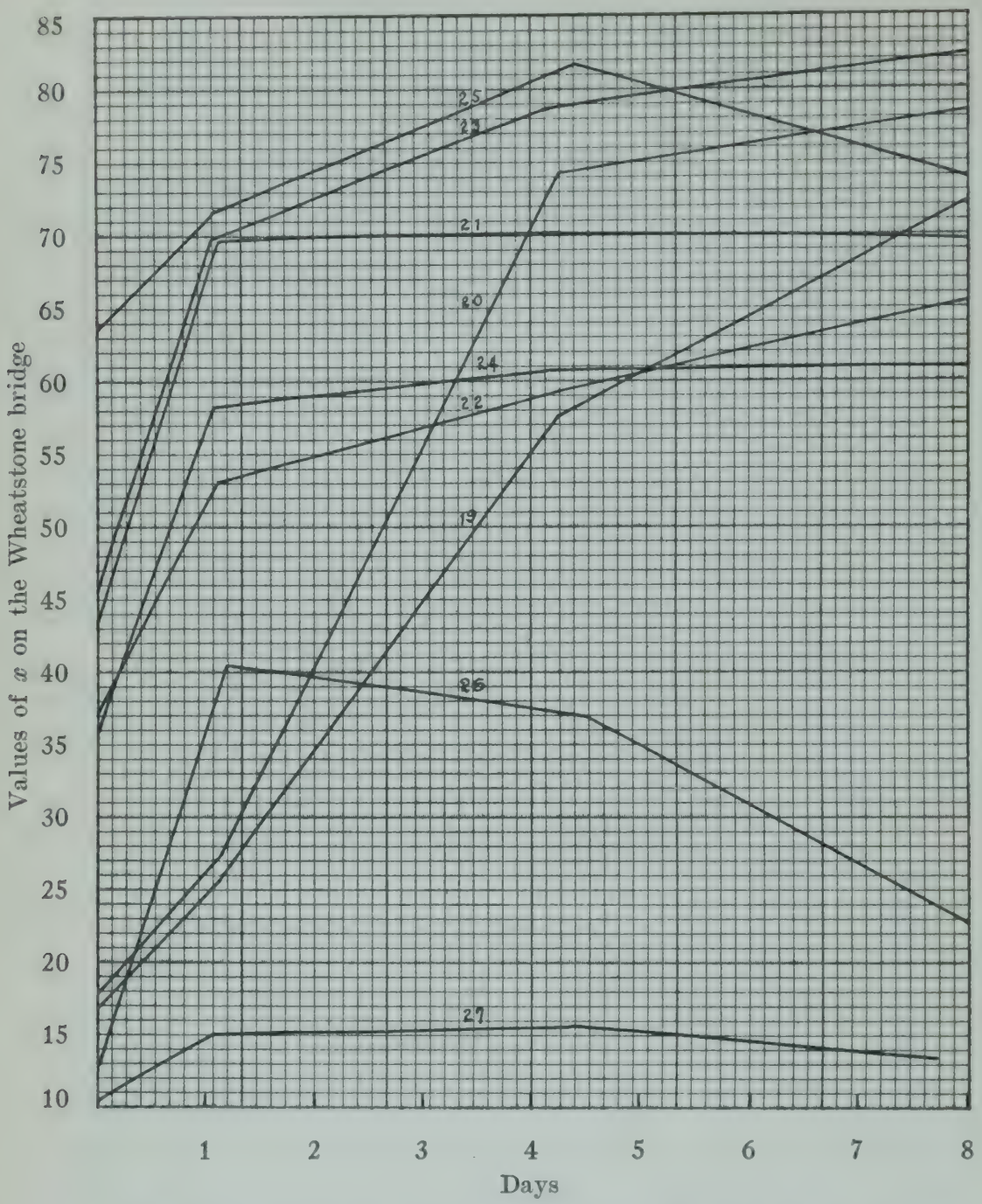

Fig. 13. Conductivity curves of cultures (series 15) in distilled water subsequent to treatment, as follows: No. 19, 4 per cent ethyl alcohol in water, 30 minutes; No. 20, 4 per cent methyl alcohol in water, 30 minutes; No. 21, 4 per cent chloral hydrate in water, 30 minutes; No. 22, 4 per cent benzol in water, 30 minutes; No. 23, 4 per cent ethyl acetate in water, 30 minutes; No. 24, 4 per cent toluene in water, 30 minutes; No. 25, 4 per cent benzaldehyde in water, 30 minutes; No. 26, control—placed directly into distilled water; No. 27, control—placed directly into distilled water. The plants were 38 days old at the time of treatment. The first reading was taken in all cases after the roots had been in distilled water exactly 30 minutes. In the case of the treated plants the roots were in distilled water containing the anesthetic for the specified time, after which they were transferred to the distilled water, the conductivity of which was subsequently determined.

previous figure. The other substances, however, even in the small concentration employed, produced a marked rise in the conductivity of the medium during the first day, after which it remained practically constant. The benzaldehyde and the

TABLE VII

CONDITION OF PLANTS EIGHT DAYS SUBSEQUENT TO TREATMENT WITH EFFECTIVE CONCENTRATIONS OF ANESTHETICS FOR A SHORT PERIOD

Culture no.	Condition of tops	Condition of roots
19	Normal and in good condition	Considerably flaccid
20	Practically normal	More flaccid than those of No. 19
21	Somewhat subnormal	Somewhat flaccid
22	Some stems considerably affected, others almost normal	Considerably flaccid
23	Practically all dead	Very flaccid
24	About the same as in No. 22	Considerably flaccid
25	Considerably subnormal	Very flaccid
26	Normal; many green, vigorous, turgid leaves	Practically normal
27	Practically normal	Normal

ethyl acetate, which themselves give a high conductivity in aqueous solution, should be considered apart from the other substances, which give no such increase. The two substances mentioned are given here merely for the purpose of comparison with the others employed. A 1 per cent solution of ethyl acetate had a conductivity of 65.2 on the Wheatstone bridge, while that of a similar solution of benzaldehyde was 88.6. These corrections should therefore be applied to the curve values in order to obtain the true value of the exosmosis from the roots in those cultures. The condition of the plants after 8 days is given in table 8.

VIII. Effects of Substances Used Singly and Combined in Pairs

It is not the writer's purpose here to go into the historical aspect of the increasingly voluminous work on toxic agents, antagonistic action, and balanced solutions, and the numerous related subjects. But since those subjects have assumed such great importance in the realm of physiology it was thought desirable to consider the effect of certain toxic and unbalanced

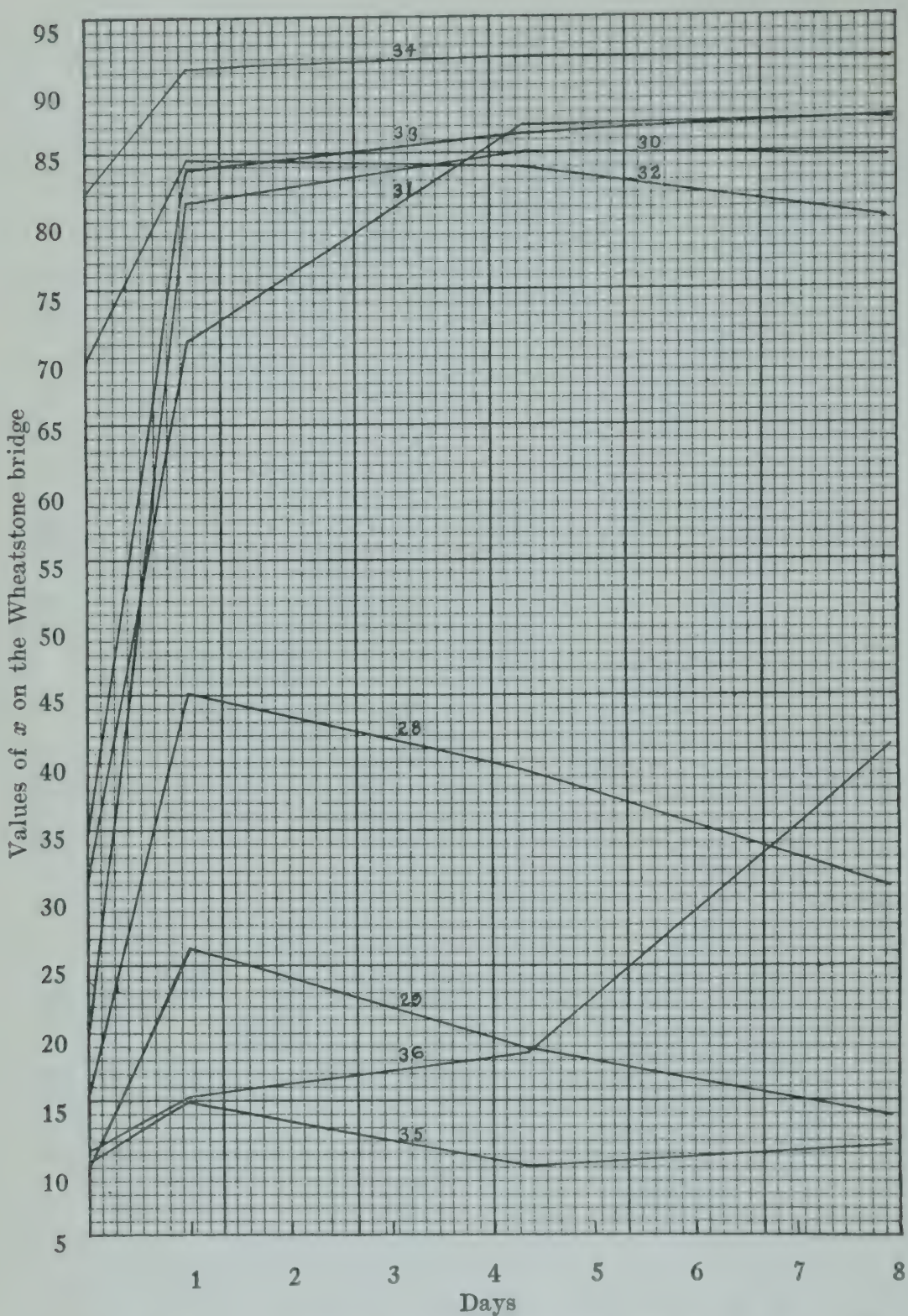

Fig. 14. Conductivity curves of cultures (series 15) in distilled water subsequent to treatment, as follows: No. 28, 1 per cent ethyl alcohol in water, to end of experiment; No. 29, 1 per cent methyl alcohol in water, to end of experiment; No. 30, 1 per cent chloral hydrate in water, to end of experiment; No. 31, 1 per cent benzol in water, to end of experiment; No. 32, 1 per cent ethyl acetate in water, to end of experiment; No. 33, 1 per cent toluene in water, to end of experiment; No. 34, 1 per cent benzaldehyde in water, to end of experiment; No. 35, control—placed directly into distilled water; No. 36, 1 per cent methyl alcohol in water, to end of experiment. The plants were 38 days old at the time of treatment. The first reading was taken in all cases after the roots had been in the distilled water containing the anesthetic exactly 30 minutes. The control, however, was exposed to the distilled water only, the first reading being taken after 30 minutes.

solutions on the exosmosis from plant roots in order to obtain a basis of comparison with the other agents used.

In this connection it might be well to consider more in detail the work of Lillie already referred to in the historical

TABLE VIII

CONDITION OF PLANTS EIGHT DAYS SUBSEQUENT TO TREATMENT WITH LOW CONCENTRATIONS OF ANESTHETICS FOR THE ENTIRE PERIOD

Culture no.	Condition of tops	Condition of roots
28	Somewhat subnormal	Slightly flaccid
29	Almost normal	Considerably flaccid; tips less flaccid than in No. 28 but upper part more so
30	Dead	Considerably flaccid
31	Almost dead	Very flaccid
32–34	Practically dead	Very flaccid
35	Practically normal	Practically normal
36	Practically normal	Somewhat flaccid

review. His work on *Arenicola* and the eggs of *Arbacia* pertains largely to the exosmosis of the pigment and the manner in which they were affected by isotonic salt solutions alone and in the presence of various anesthetics. From the effect observed, he concluded that the salts have a permeability-increasing effect on the plasma membrane which is counteracted by the anesthetics. But in dealing with the question of permeability it would seem that we must take into consideration the effect on the exosmosis, not only of any contained pigment, but of electrolytes as well.

It would have been exceedingly interesting, and would have furnished a means of strengthening or shattering his hypothesis, as the case might be, had Lillie also measured the electrical conductivity of the medium in which the Arenicola larvae and the Arbacia eggs were placed and thus determined whether the electrolytes contained in these organisms behaved as did the pigment. It would seem that the work of Loeb ('03), Peters ('04), and others might be considered as suggesting possibilities for electrolytic determinations along this line with marine organisms. Without such facts at hand any general conclusions in regard to permeability effects based on the coloring matter only must be considered imperfect. What

the reaction may be between the anesthetics and the larval pigment is another question which Lillie does not touch upon. In a recent article Miss Wheldale ('14), in discussing the natural and artificial extracts of plants, states that whereas artificial anthocyanin is soluble in ether the natural anthocyanins are not. May we not have a similar effect in the pigments concerned? Small amounts of the anesthetics may render those pigments insoluble and in that manner prevent their exosmosis rather than by bringing about any considerable alteration of the membrane; larger amounts of the anesthetics would act chemically on the membrane to a point of disintegration sufficient for the physical escape of the pigment.

It will be seen from the following experiments that in the case of roots of *Pisum sativum* certain salts caused a marked exosmosis of electrolytes. In the presence of anesthetics this exosmosis was not decreased or prevented, as Lillie found in the case of the pigments referred to, but was even increased. Hence these results do not indicate any permeability-decreasing action on the part of the anesthetics and are therefore in harmony with the findings of Dixon and Atkins ('13) and others. Another interesting condition is seen in the exosmosis resulting from single and combined salts acting for different periods of time. It was expected that such results would correspond with those obtained on plant-growth studies of antagonistic action between various nutrient and non-nutrient salts. That equally as high, or in some cases higher, exosmosis values were obtained from combined salts as from single salts is an unexpected and interesting result.

As previously indicated, the method used was to place the plants in the various solutions for the period specified and then transfer them, after careful rinsing of the roots, to distilled water in which the conductivity readings were to be taken. It was ascertained that the rinsing was effective in removing electrolytes from the roots. Figures 15 and 16 show the results for the briefer treatments with certain salts, and it is there seen that for a period of treatment less than 17 hours the N/20 $MgCl_2$ has no effect. While in the case of the culture treated for one-half hour with the $MgCl_2$, the conductivity

reading was higher at the end of four days than in the other cultures (2–5) of that group, and continued higher throughout, this fact loses its significance, as far as comparative effects are concerned, when the curve resulting from a 4-hour

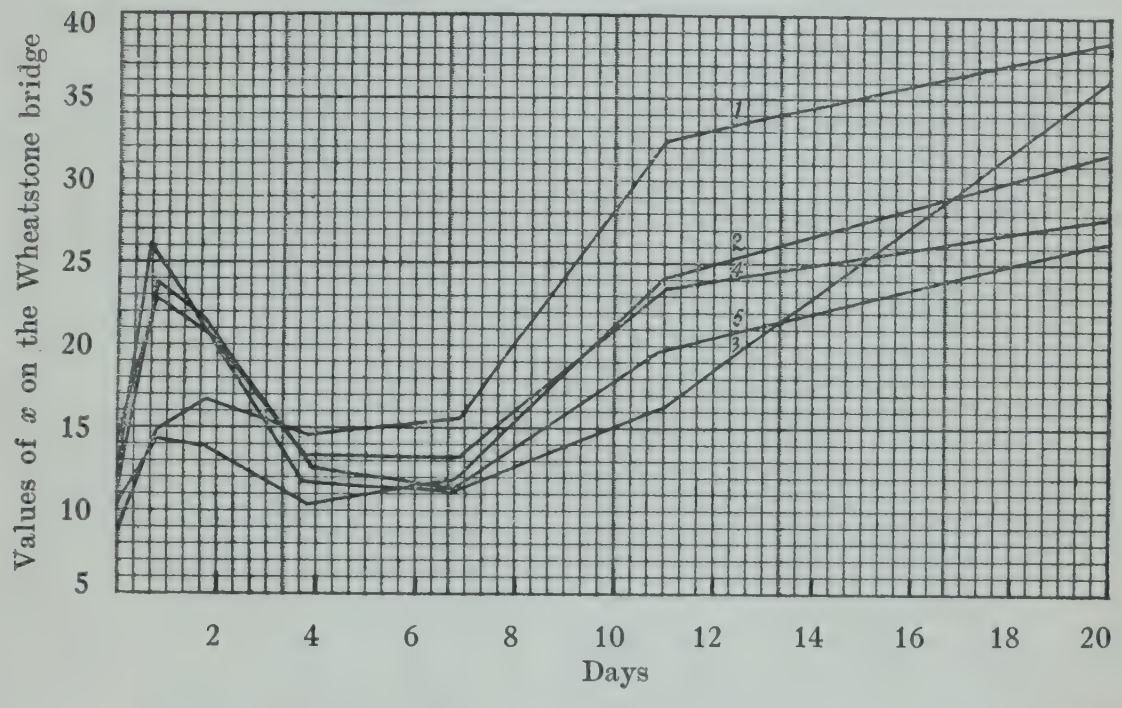

Fig. 15. Conductivity curves of cultures (series 16) in distilled water subsequent to treatment, as follows: No. 1, N/20 $MgCl_2$, 30 minutes; No. 2, N/20 $CaCl_2$, 30 minutes; No. 3, N/20 $MgCl_2$ plus N/20 $CaCl_2$, 30 minutes; No. 4, control—placed directly into distilled water; No. 5, N/20 $MgCl_2$, 4 hours. The cultures were 17 days old at the time of treatment. The first reading was taken in all cases after the roots had been in the distilled water exactly 30 minutes.

treatment with $MgCl_2$ is considered, and should no doubt be interpreted as an individual variation irrespective of treatment. In the case of No. 6, however, the curve for which represents the results of a 17-hour treatment with N/20 $MgCl_2$, we no doubt have a real effect clearly distinguished from the controls.

At the end of 20 days in distilled water following the treatment the tops of Nos. 1–10 were all in about the same condition, those of the treated plants showing no injury. Likewise the roots of Nos. 1–5 and 8–10 were practically normal, with no, or only very slight, flaccidity; those of No. 6, however, were brownish in color and somewhat flaccid, while those of

No. 7 were brownish only in spots, but were of about the same flaccidity as those of No. 6.

Having found that a treatment of 17 hours under the conditions indicated above was not sufficient to yield the most

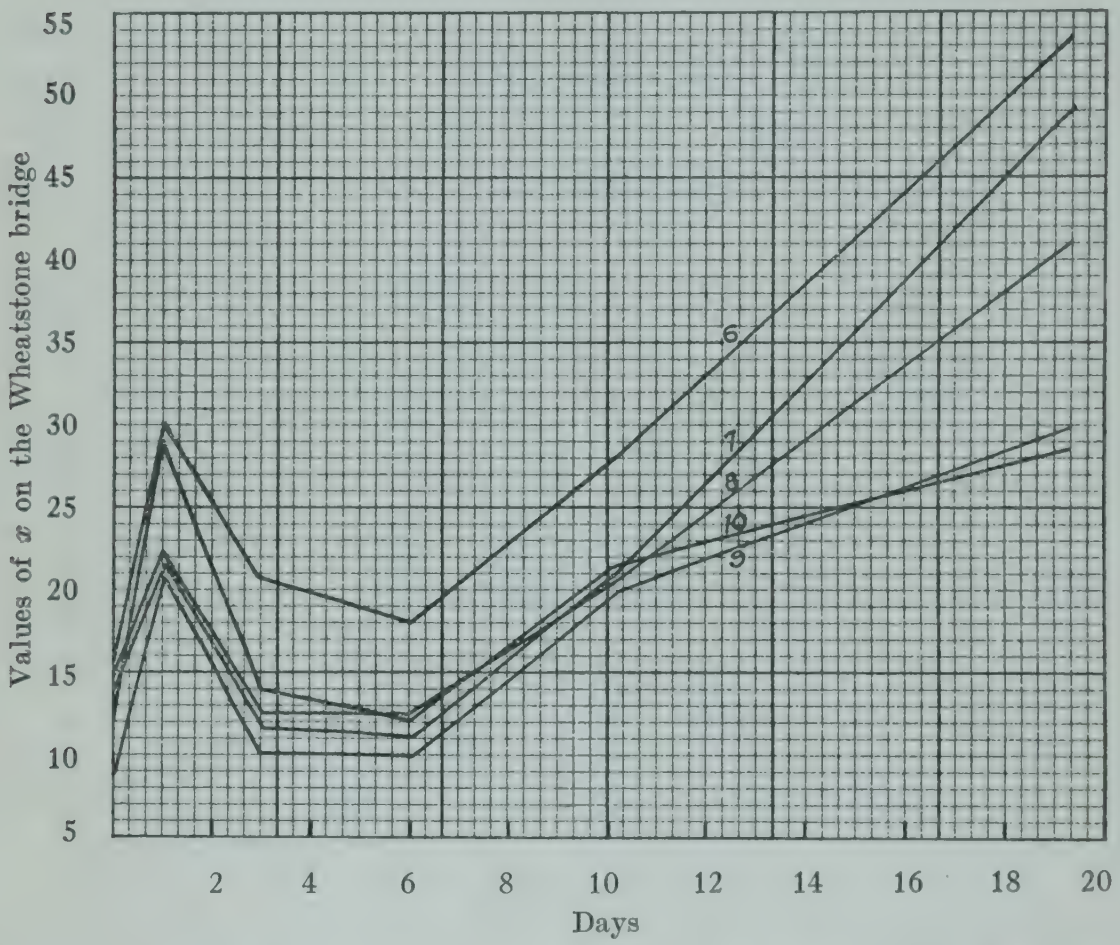

Fig. 16. Conductivity curves of cultures (series 16) in distilled water subsequent to treatment, as follows: No. 6, N/20 $MgCl_2$, 17 hours; No. 7, N/20 $CaCl_2$, 17 hours; No. 8, N/20 $MgCl_2$ plus N/20 $CaCl_2$, 17 hours; No. 9, control—distilled water, renewed after 17 hours; No. 10, control—distilled water, not renewed. The cultures were 17 days old at the time of treatment. The first readings were taken in all cases after the roots had been in the distilled water exactly 30 minutes. No. 10 remained in the full nutrient solution until the treated cultures were transferred (after the 17-hour period) from the respective solutions to distilled water.

positive results, it was decided to try stronger concentrations and longer periods. Figure 17 shows the conductivity curves after a period of treatment extending 75 hours. Some interesting results were obtained. N/10 $MgCl_2$ gave the highest readings, closely followed by N/10 $MgCl_2$ plus N/10 $CaCl_2$; the N/20 $MgCl_2$ plus N/20 $CaCl_2$ curve is very similar to that

obtained from N/10 $MgCl_2$ plus N/20 $CaCl_2$, while the N/10 $MgCl_2$ plus N/100 $CaCl_2$ causes a rise higher than that in the two curves just mentioned after the fifth day. It was unexpected that N/20 $CaCl_2$ should exceed N/20 $MgCl_2$ in its

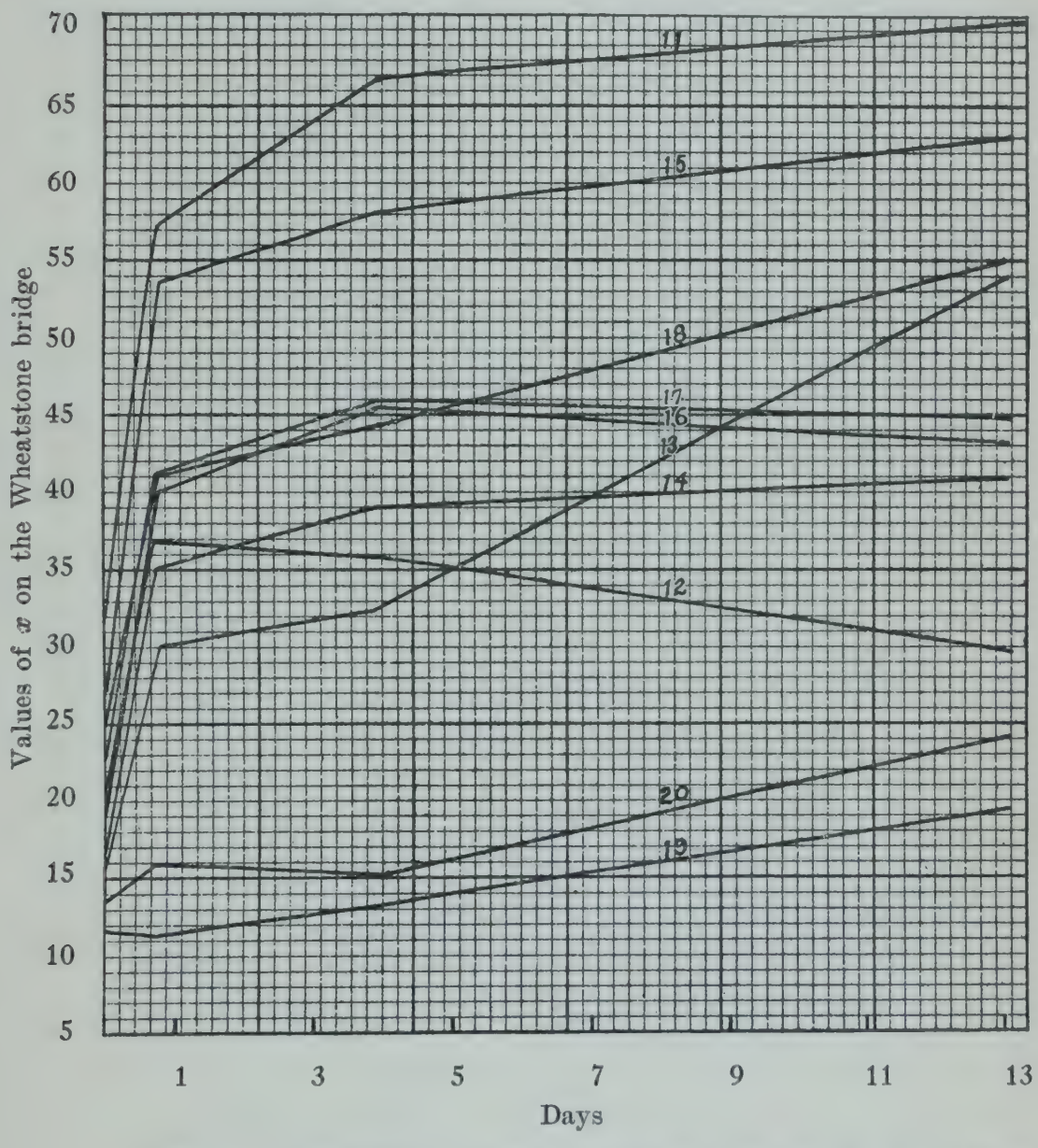

Fig. 17. Conductivity curves of cultures (series 16) in distilled water subsequent to treatment, as follows: No. 11, N/10 $MgCl_2$, 75 hours; No. 12, N/20 $MgCl_2$, 75 hours; No. 13, N/10 $CaCl_2$, 75 hours; No. 14, N/20 $CaCl_2$, 75 hours; No. 15, N/10 $MgCl_2$ plus N/10 $CaCl_2$, 75 hours; No. 16, N/20 $MgCl_2$ plus N/20 $CaCl_2$, 75 hours; No. 17, N/10 $MgCl_2$ plus N/20 $CaCl_2$, 75 hours; No. 18, N/10 $MgCl_2$ plus N/100 $CaCl_2$, 75 hours; No. 19, control—distilled water, renewed after 75 hours; No. 20, control—distilled water, not renewed. The plants were 21 days old when treated. The first reading was taken after the roots had been in the distilled water exactly 30 minutes (in No. 20, 75 hours). Nos. 19 and 20 were placed in distilled water at the same time that the cultures to be treated were placed in their respective solutions.

effect on exosmosis and that the conductivity curve resulting from treatment with N/10 $CaCl_2$ should rise so high at the end.

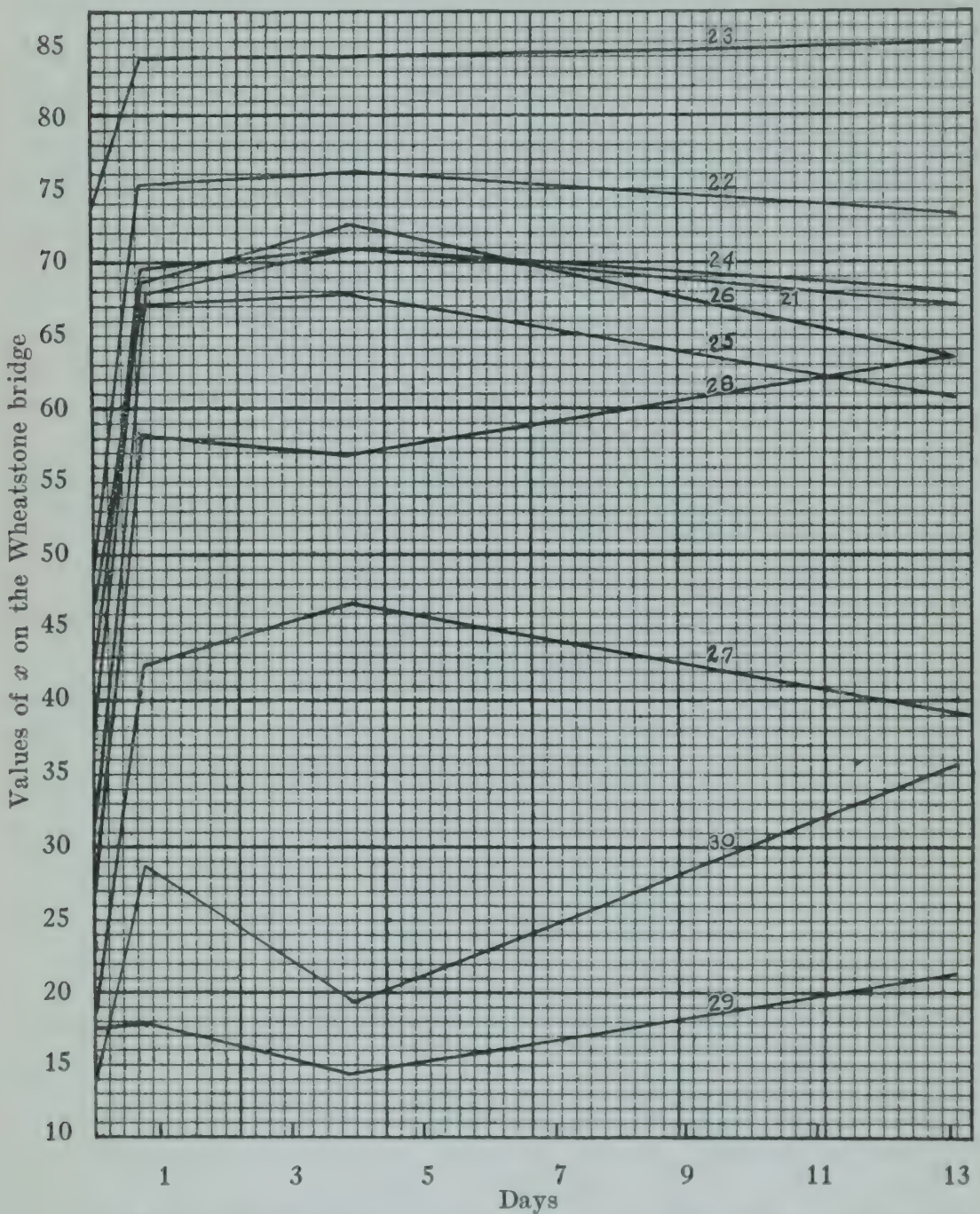

Fig. 18. Conductivity curves of cultures (series 16) in distilled water subsequent to treatment, as follows: No. 21, N/10 NaCl, 75 hours; No. 22, N/10 KCl, 75 hours; No. 23, N/10 NaCl plus N/10 KCl, 75 hours; No. 24, N/20 NaCl plus N/20 KCl, 75 hours; No. 25, N/10 NaCl plus N/10 $CaCl_2$, 75 hours; No. 26, N/10 KCl plus N/10 $CaCl_2$, 75 hours; No. 27, N/20 NaCl, 75 hours; No. 28, N/20 KCl, 75 hours; No. 29, control—distilled water, not renewed; No. 30, control—distilled water, not renewed. The plants were 21 days old when treated. The first reading was taken after the roots had been in the distilled water 30 minutes (in No. 29, 75 hours). Culture 30 was placed in distilled water at the end of the 75-hour period, having been in full nutrient solution up to that time.

At the end of 13 days in distilled water following the treatment, the tops of Nos. 11–20 were of the same appearance throughout, i. e., normal. The roots were also practically normal in the case of Nos. 12–20, except for a brownish color on those of Nos. 12, 13, 15, and 16–18, being especially evident in the case of No. 15. In addition to being brown, however, the roots of No. 11 were considerably flaccid.

Figure 18 shows similar relations for NaCl, KCl, and $CaCl_2$. It is seen that KCl is more effective than NaCl in causing exosmosis. Far from ameliorating the exosmotic condition, the treatment with combined NaCl and KCl likewise yields high conductivity readings of the medium, the N/10 concentration of each combined giving the highest. It can not be argued that this effect is due solely to the osmotic pressures of the solutions of the agents in question, for if that were the case we should expect more comparable results on the basis of the osmotic effects of the various solutions at the concentrations used. There is a reduction in the effect when the NaCl and KCl used singly are reduced to concentrations of N/20.

The condition of the plants 16 days after first applying the treatment, or 13 days after being in distilled water, is shown in table IX, from which it is evident that there was great exosmosis with but little or no visible effect accompanying it.

TABLE IX

CONDITION OF PLANTS TREATED WITH VARIOUS SALTS FOR DIFFERENT PERIODS OF TIME

Culture no.	Condition of tops	Condition of roots
21 and 22	Normal	Slightly brown and very slightly flaccid
23	Dead—badly wilted at end of treatment	Very limp and flaccid and brownish
24–28	Normal	Very slightly brownish but practically normal
29 and 30	Normal	Practically normal

That osmotic effects play practically no part in the phenomenon under consideration is indicated from the results of Loeb ('03) on *Gammarus* and those of True ('14) on Lupinus seedlings. The writer also performed experimental work to

determine this point. Solutions of pure saccharose of varying concentrations were used and the effects produced by the same during a period of 24 hours as compared with pure distilled water, measured by the determined conductivity of the medium both during the 24 hours and after (when the plants which had been in the sugar solutions were also placed in distilled water). These results are given in table x. As there seen, no differences were obtained from the different concentrations.

TABLE X

EXOSMOSIS FROM THE ROOTS OF PLANTS IN SUGAR SOLUTIONS AND DISTILLED WATER *

Time of readings	Culture 1 1.28% saccharose sol'n. 24 hours followed by dist. H_2O	Culture 2 2.56% saccharose sol'n. 24 hours followed by dist. H_2O	Culture 3 5.13% saccharose sol'n. 24 hours followed by dist. H_2O	Culture 4 control dist. H_2O throughout changed every day conductivity readings
Conductivity readings of the sugar solutions:				
Before roots placed in the solution	9.4	10.6	10.9	10.9
After 10 hrs	28.0	19.7	30.8	32.9
After 24 hrs	28.9	18.3	29.0	32.9
Increase over original sol'n. during 24 hrs	19.5	7.7	18.1	22.0
Conductivity readings of the distilled water:				
After ½ hr	9.4	8.6	8.8	8.3
After 23 hrs	10.5	11.5	11.0	10.4
After 48 hrs	10.9	11.3	10.2	10.0
Increase over dist. H_2O the first half hour †	3.4	2.6	2.8	2.3
Increase over dist. H_2O during 48 hours †	4.9	5.3	4.2	4.0

* All readings represent values of x on the Wheatstone bridge, the resistance in the box being 9,110 ohms.

† The average reading of the distilled water before placing roots in it was approximately 6.0.

In table xi are shown the effects produced by salts alone as well as by salts plus anesthetics in weak concentrations. It was desired to use approximately the same concentrations of anesthetics as indicated by the work of Lillie ('12), Osterhout ('13), and others. The conductivity of the water containing the anesthetics was not determined after the 53-hour treatment and hence the resulting exosmosis during that interval was not ascertained. But from other experiments on

the effect of anesthetics in solution we have seen that the exosmosis is rapid and considerable during the first day or so and then remains stationary, i. e., the curve becomes hori-

TABLE XI

EFFECTS OF SALT SOLUTIONS USED SINGLY AND COMBINED WITH ANESTHETICS UPON THE EXOSMOSIS FROM THE ROOTS OF PLANTS (PLANTS 40 DAYS OLD WHEN TREATED)

Culture no.	Treatment	Conductivity*				
		Readings		Increase over dist. H_2O**		
		After ½ hr.	After 42 hrs.	1st ½ hr.	Next 41½ hrs.	Total in 42 hrs.
31	N/10 $MgCl_2$, 53 hrs.....	35.4	57.1	29.4	21.7	51.1
32	N/10 NaCl, 53 hrs.....	34.4	60.9	28.4	26.5	54.9
33	N/10 KCl, 53 hrs.....	40.8	63.0	34.8	22.2	57.0
34	0.7% ether in H_2O, 53 hrs.....	10.0	11.6	4.0	1.6	5.6
35	0.7% $CHCl_3$ in H_2O, 53 hrs.....	12.1	36.3	6.1	24.2	30.3
36	0.7% benzol in H_2O, 53 hrs.....	11.3	17.7	5.3	6.4	11.7
37	N/10 $MgCl_2$ and 0.7% ether, 53 hrs.....	41.2	64.7	35.2	23.5	58.7
38	N/10 $MgCl_2$ and 0.7% $CHCl_3$, 53 hrs.....	45.5	57.2	39.5	11.7	51.2
39	N/10 $MgCl_2$ and 0.7% benzol, 53 hrs.....	44.0	49.4	38.0	5.4	43.4
40	N/10 NaCl and 0.7% ether, 53 hrs.....	37.4	59.5	31.4	22.1	53.5
41	N/10 NaCl and 0.7% $CHCl_3$, 53 hrs.....	47.5	62.4	41.5	14.9	56.4
42	N/10 NaCl and 0.7% benzol, 53 hrs.....	49.5	56.0	43.5	6.5	50.0
43	N/10 KCl and 0.7% ether, 53 hrs.....	50.2	76.0	44.2	25.8	70.0
44	N/10 KCl and 0.7% $CHCl_3$, 53 hrs.....	51.7	65.4	45.7	13.7	59.4
45	N/10 KCl and 0.7% benzol, 53 hrs.....	49.2	55.8	43.2	6.6	49.8
46 and 47	Control (dist. H_2O renewed after 53 hrs.)...	10.9	11.9	4.9	1.0	5.9
48	Control (dist. H_2O not renewed).....	15.2†	15.5‡	9.2§	.3	9.5‖
49 and 50	Control (full nutr. until Nos. 31–45 were placed in dist. H_2O).....	12.5	39.0	6.5	26.5	33.0

* All readings represent values of x on the Wheatstone bridge with a resistance in the box of 9,110 ohms.

** The average reading of the distilled water before placing roots in it was approximately 6.0.

† After 53 hours. ‡ After 95 hours. § In 53 hours. ‖ In 95 hours.

zontal. We can therefore safely infer that such was the case here, except possibly in the ether-treated cultures in which the roots and tops showed no effect whatever from the treat-

ment. We can thus account for the fact that the increase in the conductivity of the medium in Nos. 34, 35, and 36, was so slight and so similar to that given by the controls. It will be seen that the anesthetics did not antagonize the salts so far as exosmosis of electrolytes is concerned. The condition of the plants after the 53-hour treatment is shown in table XII.

TABLE XII

CONDITION OF PLANTS FIFTY-THREE HOURS AFTER TREATMENT WITH SOLUTIONS OF SALTS AND ANESTHETICS

Culture no.	Condition of tops	Condition of roots
31	Normal	Yellowish brown, somewhat flaccid
32	Practically normal	Slightly yellow, practically normal
33	Subnormal, drying considerably	Slightly yellow, practically normal
34	Normal	Practically normal
35	Normal	White, but considerably flaccid
36	Almost normal	Very flaccid
37	Practically normal	Yellowish and considerably flaccid
38	Almost normal	Somewhat flaccid
39	Drying considerably	Very flaccid
40	Normal	Almost normal
41	Drying somewhat	Considerably flaccid
42	Drying considerably	Very flaccid
43	Practically normal	Practically normal
44	Drying considerably	Considerably flaccid
45	Drying badly	Very flaccid
46–50	Normal	Practically normal

The concentration of the anesthetics used in the above experiments was near the boundary which would just produce exosmosis. To eliminate such action entirely when these substances were used alone, therefore, the concentrations used were reduced to a point below that at which they cause exosmosis to any appreciable extent, if at all. The results of that series are given in table XIII, where we see again no indications that there is any decreasing effect by the anesthetics on the exomosis induced by salts. On the contrary, the combined salt and anesthetic cause a greater exosmosis than the salt alone.

As measured by the resulting growth of roots, Hibbard ('13) found an antagonistic action between $CuSO_4$ and chloral hydrate. To determine if such action would also hold true in

the case of exosmosis, an experiment was set up, the results of which are given in table XIV. As there seen, there was no decrease in the exosmosis caused by either substance when the two were combined.

TABLE XIII

EFFECTS OF SALT SOLUTIONS USED SINGLY AND COMBINED WITH ANESTHETICS ON THE EXOSMOSIS FROM THE ROOTS OF TREATED PLANTS*

Culture no.	Treatment	Conductivity				
		Readings		Increase over dist. H_2O‖		
		After ½ hr.	After 41 hrs.	1st ½ hr.	Next 40½ hrs.	Total in 41 hrs.
1	1/8 saturated $CHCl_3$ in H_2O, 44 hrs	8.5†	11.0	2.5‡	2.5	5.0
2	M/200 chloral hydrate, 44 hrs	13.4†	18.9	7.4‡	5.5	12.9
3	N/10 NaCl, 44 hrs	38.4†	59.3	32.4‡	20.9	53.3
4	N/10 KCl, 46 hrs	53.6	76.2	47.6	22.6	70.2
5	1/8 saturated $CHCl_3$ in H_2O & N/10 NaCl, 44 hrs	46.2	61.6	40.2	15.4	55.6
6	1/8 saturated $CHCl_3$ & N/10 KCl, 46 hrs	47.2	76.5	41.2	29.3	70.5
7	M/200 chloral hydrate & N/10 NaCl, 46 hrs	49.1	79.3	43.1	30.2	73.3
8	M/200 chloral hydrate & N/10 KCl, 46 hrs	60.5	84.2	54.5	23.7	78.2
9	N/10 NaCl & N/10 KCl 46 hrs	70.7	82.7	64.7	12.0	76.7
10	N/20 NaCl & N/20 KCl, 46 hrs	41.8	71.7	35.8	29.9	65.7
11	Control (dist. H_2O renewed every 2 days)	11.4	10.8	5.4	−.6	4.8
12	Control (dist. H_2O not renewed)	16.7	25.0	10.7	8.3	19.0

* All readings represent values of x on the Wheatstone bridge with a resistance in the box of 9,110 ohms.

† Reading taken after 50 minutes. ‡ Increase in first 50 minutes.

‖ The average reading of the distilled water before placing roots in it was approximately 6.0.

Merely to get a basis of comparison between the effects produced by the various agents above mentioned and acid and alkali in certain concentrations, plants were placed in solutions of KOH and H_2SO_4 of approximately the limiting concentrations for root growth, as found by Kahlenberg and True ('96). Instead of excretion being greater than absorption the reverse was found to be true during the period the plants remained in the solutions. The plants, to all external appearances, were not affected adversely in the least, and when later

placed in distilled water gave practically no greater exosmosis than the control. With stronger concentrations a marked effect would undoubtedly be produced. The results obtained are given in table xv. Another point worthy of note in this

TABLE XIV

EFFECTS OF COPPER SULPHATE AND CHLORAL HYDRATE USED SINGLY AND COMBINED UPON THE EXOSMOSIS FROM THE ROOTS OF PLANTS

Cult. no.	Treatment	Specific conductivity of the sol'ns.*			Values of x,† or bridge readings of the Distilled Water				
		Before roots in the sol'n.	After 27 hrs. in the sol'n.	Increase in 27 hrs.	After ½ hr. in the H_2O	After 63 hrs. in the H_2O	Increase the 1st ½ hr. ‡‡	Increase the next 62½ hrs.	Total increase in 63 hrs. ‡‡
1	M/10,000 $CuSO_4$, 28 hrs.....	2.92	16.68	13.76	19.7	55.4	13.7	35.7	49.4
2	M/100 $CuSO_4$, 27 hrs.....	142.40	151.10	8.70	22.0	22.4	16.0	.4	16.4
3	M/8,000 chloral hydrate, remaining to end of exp.....	.35	1.16	.81	20.6‡	13.1**	14.6§	−7.5	7.1**
4	M/100 chloral hydrate, 26 hrs...	.37	3.04	2.67	14.8	16.8	8.8	2.0	10.8
5	M/10,000 $CuSO_4$ and M/8,000 chloral hydrate, 26 hrs.....	2.82	19.77	16.95	15.0	53.3	9.0	38.3	47.3
6	M/100 $CuSO_4$ and M/100 chloral hydrate, 26 hrs.	82.69	95.25	12.56	17.2	20.2	11.2	3.0	14.2
7	Control (dist. H_2O, changed every 4 days).....	.32	.79	.47	15.0‖	12.9††	9.0§	−2.1	6.9††
8	Control (dist. H_2O, not changed)...	.....	.....	.....	14.8	10.7	8.8	−4.1	4.7

* The values given are to be multiplied by 10^{-5} to obtain specific conductivity values.

† Resistance in box 9,110 ohms.

‡ After 26 hours in the solution.

§ The first 26 hours.

‖ After 26 hours in distilled H_2O.

‡‡ The average reading of the distilled water before placing roots in it was approximately 6.0.

** After 89 hours in the solution.

†† After 89 hours in the water.

connection and seen in table xv is the additional verification of the fact that the rinsing method used throughout this investigation was effective and that no electrolytes were carried

over on the roots from the full nutrient solutions, salt solutions, and other media to the distilled water, at least not in sufficient quantity to affect the validity of the results in any way. Although the conductivity of the acid and alkaline media was very high, it is seen by reference to table xv that after rinsing the roots in the usual manner and transferring the cultures to distilled water the readings were very low, thus showing that practically no electrolytes were carried over on the roots.

TABLE XV

CONDUCTIVITY READINGS OF THE CULTURE MEDIA OF PLANTS IN KOH, H_2SO_4, AND LATER IN DISTILLED WATER

Cult. no.	Treatment	Specific conductivity* of the sol'ns.				Values of x,† or bridge readings of the distilled water				
		Before roots in the sol'n.	After 22 hrs. in the sol'n.	After 47 hrs. in the sol'n.	Increase in 47 hrs.	After ½ hr. in the H_2O	After 50 hrs. in the H_2O	Increase the 1st ½ hr.††	Increase the next 49½ hrs.	Total increase in the 50 hrs.††
1	N/12,800 H_2SO_4, 47 hrs.....	2.39	1.50	1.03	−1.36	10.8	10.5	4.8	−.3	4.5
2	N/6,400 H_2SO_4, 47 hrs.....	5.62	2.53	1.17	−4.45	8.7	9.6	2.7	.9	3.6
3	N/400 KOH, 47 hrs.....	42.02	20.09	16.39	−25.63	11.5	8.7	5.5	−2.8	2.7
4	N/200 KOH, 47 hrs.....	58.50	27.98	24.16	−34.34	11.2	10.5	5.2	−.7	4.5
5	Control (dist. H_2O, not changed)...	.98	2.56	1.32	.34	22.8‡	17.8**	16.8‡	−5.0	11.8**

* The values given are to be multiplied by 10^{-5}.
† The resistance in the box was 9,110 ohms.
‡ After being in distilled water 47 hours.
†† The average reading of the distilled water before placing roots in it was approximately 6.0.
** After 97 hours.

IX. General Discussion

In the foregoing experiments we have been able to note the exosmosis of electrolytes following different treatments. As compared with the controls we have seen marked excretions in some cases and slight or no exosmosis in excess of that in the controls in others. In the normal untreated cultures, or controls, we have seen that there is almost universally a slight exosmosis from the roots into the distilled water for about 24

hours or so, and then in most cases there is a decline in the conductivity curve to a point approaching the original position, after which there may or may not be a gradual incline, depending, probably, on various factors.

It might be well briefly to consider some theoretical aspects of the subject, especially in regard to the causal agencies effecting the increased exosmosis of the treated cultures. The mere transfer of a culture from a full nutrient solution to distilled water is not in itself sufficient to account for the effects produced, as we have seen that osmotic effects play little or no rôle in this connection, a conclusion in harmony with the findings of Loeb ('03) and of True ('14). To what then is the exosmosis due? Can it all be laid at the door of cell cytolysis? What influence has an alteration of the plasma membrane?

In any case, we are dealing with the effect of physical and chemical factors upon the plant cell. For our purpose here it is not considered necessary to enter upon a discussion of the various ideas regarding the details of the structure of the cell and its limiting membrane, or the work and theories of the different investigators on both the animal and plant side concerning the permeability of the plasma membrane. Yet in passing, it may be well to mention Overton's theory regarding the lipoid nature of the plasma membrane, Nathansohn's idea of a mosaic structure of the same, Czapek's experiments indicating the presence of neutral fats in the membrane, Lepeschkin's view that the plasma membrane is a continuous film (some of the work of the last two investigators being summarized by Blackman, '12), and Kite's work on the structure of protoplasm, and also make note of the recent work of Cranner ('14) on the lipoid content of the cell wall.

The effect of the two physical factors, heat and cold, may undoubtedly be considered as resulting in a complete or incipient disorganization of the cell, depending upon the duration of exposure, and a consequent escape of some of the contents into the surrounding medium.

In the case of the various chemical factors or agents used the matter is probably not so simple or so easily disposed of. However, a conception that would fulfill the requirements

theoretically and also accord with the experimental results would seem to be based on the specificity of chemical reaction. The cell, with its complex aggregation of chemical substances, may be considered as interacting with the substance employed, be it anesthetic, toxic agent, salt solution, or other chemical. It may be assumed that each substance has a greater affinity (if we may use that tabooed chemical term) for a particular component of the cell than for other constituents and hence reacts accordingly. This was exemplified by the striking comparison between the effect produced by anesthetics in certain concentrations and that produced by the KCl or NaCl solution. The exosmosis, it is true, was considerable in both cases, but the resulting appearance of the roots was markedly different, the anesthetics causing indications of flaccidity, while the roots exhibiting quite as much exosmosis in the salt solutions, remained practically normal. If we assume that the anesthetic acted upon the colloidal matrix or gel portion of the cell and thus more or less destroyed its organization, while the salts reacted with the substances in the sol condition and left the matrix more or less intact, we would seem to have a basis for explaining the differences observed.

Anesthesia has been considered by Lillie, Osterhout, and others to be essentially a reversible process, provided that the concentration of the anesthetic was not sufficient to be toxic. The experimental work reported herewith, however, on the excretion of electrolytes induced by various anesthetics does not seem to substantiate that view. If the concentration of the anesthetics employed was below a certain point there was no observable effect whatsoever. By increasing the concentration the critical point was attained when excretion began, and as the concentration of the anesthetic was further increased, or as the period of application was lengthened, excretion likewise increased. The excretion process induced by anesthetics therefore conformed in every way to an irreversible chemical reaction. In Osterhout's conductivity measurements of tissue, secondary agglutinization phenomena may possibly have entered in to give the observed effects, and thus have masked the real chemical reaction. Recovery of organ-

isms after anesthetic treatment has also been considered by some as evidence indicating the reversibility of the anesthetic action. If such be viewed from the standpoint of chemical reactions, however, the mere fact of recovery of the organism to a normal condition following the application of anesthetics would not seem to be sufficient justification for concluding that the chemical reaction which initiated the effect is a reversible one, especially when one considers the manifold activities of the cell and the wonderful recuperative powers possessed by organisms, these no doubt involving numerous reactions. Hence the writer is inclined to the belief that an irreversible chemical reaction was at the basis of the phenomena observed as a result of the treatment of the plant with anesthetics and the consequent exosmosis of substances contained in the cell, and that any alteration of the plasma membrane resulting in changed permeability finds its best explanation on the basis of actual chemical reactions.

It is further believed that the results obtained by antagonistic pairs of salts and by single salts are also to be explained, as far as resulting exosmosis is concerned, in the specificity of the action of each. The method employed herein gives a delicate register of such action and is considered to be especially desirable because in it growth phenomena, with their resulting complex nutritive relations, may be left out of consideration. That the high conductivity readings in the case of the salts and certain other electrolytes was not due to insufficiency of the washing before the roots were placed in the distilled water was abundantly proved in various ways.

In regard to the method of experimentation employed in the work here reported, mention may well be made of its adaptability for delicate determinations pertaining to the relative toxicity of different substances. In the past such determinations have been made by means of growth measurements. It would seem that in this method we have, in some respects, a more rapid and satisfactory procedure for such work.

X. Summary and Conclusions

A brief historical review is given of the subject of excretion

from plant roots, exosmosis from living cells, and of excretion from leaves and other tissues.

The methods of experimentation are described.

A theoretical discussion is given of the various aspects of the subject.

The following are some of the experimental results obtained:

(a) Pea seedlings grew better in distilled water in which exosmosis from the previously treated plants of the first crop had occurred than in fresh distilled water, or in distilled water in which untreated plants had been grown.

(b) Peas and horse beans did not do as well in distilled water in which pea seedlings had already grown for 21 days as in fresh distilled water.

(c) Abundant exosmosis may occur from treated plants, even though the roots remain entirely normal in appearance. When the tops were badly affected and the roots remained normal, abundant exosmosis also occurred and the indications pointed in some cases to a downward flow of substances into the roots and out into the aqueous medium. No conclusive proof of this was obtained, however.

(d) Anesthetic vapors cause marked exosmosis upon considerable exposure of the plants to them, but there is none if the exposure be short. The interval required to initiate exosmosis was accurately determined. The order of effectiveness of the vapors tried is, ether, least; illuminating gas, more; and chloroform, most.

(e) The time limits for the exposure of plants to extremes of temperature in relation to exosmosis were determined. Comparison was also made between the effect of dry and moist heat.

(f) The exosmosis curves for various organic compounds were found. In general, at the concentrations used, marked excretion was produced.

(g) The effects of single salts, salts in pairs, and salts plus anesthetics in solution were ascertained as regards the exosmosis produced upon the plants in such solutions. Antagonistic relations in the sense of one substance decreasing the

exosmotic effect produced by another substance were found not to hold in the cases tried and under the conditions of the experiment.

It is with pleasure that the writer acknowledges his indebtedness to Dr. B. M. Duggar for numerous helpful suggestions in the prosecution of this work, and to Mrs. Amy Lyman Merrill for valuable assistance in the calculations involved and in the plotting of the curves; also to Dr. J. R. Schramm, who kindly aided in the tedious work of preparing the manuscript for the printer.

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MONOGRAPH OF THE NORTH AND CENTRAL AMERICAN SPECIES OF THE GENUS SENECIO—PART II[1]

J. M. GREENMAN

Curator of the Herbarium of the Missouri Botanical Garden
Associate Professor in the Henry Shaw School of Botany of Washington University

Introduction

The study upon which this monograph is based was begun nearly twenty years ago, at which time the author was an Assistant at the Gray Herbarium of Harvard University. Nearly every collection of any considerable size which came to the Herbarium, particularly from western United States, Mexico, and Central America, contained specimens of *Senecio,* many of which were either undetermined or referred doubtfully to some obscure or little known species. The identification of such material was often a laborious task, since all species recorded from a given region had to be listed and then specific identity established by a process of elimination. The available publications for such work were De Candolle's 'Prodromus,' Gray's 'Synoptical Flora,' and Hemsley's splendid contribution to the systematic literature of the botany of Mexico and Central America in the 'Biologia Centrali-Americana'; but the results obtained were often very unsatisfactory, because of the large number of new species published in scattered papers during the two decades following the appearance of the 'Synoptical Flora' and the 'Biologia.'

It was felt, therefore, that a revision of the genus, in the light of recent and more complete collections, which have accumulated from the numerous botanical explorations in different parts of North America, would be helpful to those concerned with this difficult group of plants and especially in the organization of material in different herbaria. A critical study of *Senecio* with the view of publishing eventually a

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monograph was suggested to me by Dr. B. L. Robinson, Curator of the Gray Herbarium, who very kindly offered to place at my disposal the entire representation of this genus in the Gray Herbarium, and who, moreover, willingly granted me the exceptional privilege of taking abroad the North American specimens, including all the types, for comparison and study in European herbaria. Accordingly nearly 2,000 mounted specimens were taken to Berlin; and through the courtesy of the authorities of the Royal Botanical Gardens and Museums of Berlin every facility in that institution, which is remarkably rich in Central and South American plants, was accorded me and work on the task was begun under the direction of Professor A. Engler.

It was necessary first of all to acquire a detailed knowledge of the general morphology of the genus *Senecio* as a whole, and also of the closely allied genera. The results of these investigations are briefly recorded in the first part of this monograph, namely 'Monographie der nord- und central-amerikanischen Arten der Gattung Senecio, I. Teil' which is frequently referred to in the following text. This preliminary work and the rich collections of the Gray and Berlin Herbaria form, therefore, the basis for the present systematic part of the monograph.

After completing my studies in Berlin I went to London, taking the Gray Herbarium specimens with me, and there spent several weeks, particularly in the examination of authentic and type specimens at the Kew Herbarium and in the Linnean Herbarium. The opportunity at Berlin, Kew, and Paris to actually compare side by side and in detail, recent specimens, or series of specimens, with many of the older types, some of which are more or less incomplete, has been of very great advantage, and, in fact, has made it possible to establish beyond doubt the identity of many of our American species.

In addition to those herbaria mentioned it also has been my good fortune to study this group of plants in several American institutions, notably the Herbarium of the Geological Survey of Canada, the United States National Her-

barium, the New York Botanical Garden Herbarium (including the Torrey Herbarium), the Herbarium of the Field Museum of Natural History, the Herbarium of the Philadelphia Academy of Natural Sciences, the Missouri Botanical Garden Herbarium, and a number of private collections. To the directors and curators of all these, as well as the owners of the private herbaria, and correspondents who have facilitated my work, I wish to express personal thanks; but I desire especially to extend most grateful acknowledgments to Dr. Benjamin Lincoln Robinson, Asa Gray Professor of Systematic Botany at Harvard University, and Geheimrath Professor Dr. Adolph Engler, Director of the Royal Botanical Gardens and Museum of Berlin, without whose coöperative interest and extreme liberality in the use of valuable scientific material under their charge, this work would have been impossible. I am also grateful to Mr. W. Botting Hemsley, of the Kew Herbarium, through whose courtesy I secured type material of certain rare Mexican species and a number of excellent drawings, some of which are herein reproduced.

I have cited exsiccatae rather freely, particularly such as occur in American herbaria, but by no means all that have been examined, and I have given even at the expense of much repetition detailed citation of specimens in different herbaria, hoping that this would be helpful in the interpretation of species and to future students of the genus. The few plates which it is possible to include are chosen to illustrate more especially the different sections as here defined.

SENECIO [TOURN.] LINN.

Senecio [Tourn. Inst. 456. *pl. 260.* 1700] L. Sp. Pl. **2**: 866. 1753; Gen. Pl., ed. 5, 373, n. 857. 1754; Hill, Hort. Kew. 25. 1768, and ed. 2, 1769; Juss. Gen. Pl. 181. 1789; Less. Syn. 391. 1832; DC. Prodr. **6**: 340. 1837; Endl. Gen. 458, n. 2811. 1838; Hook. Fl. Bor. Am. **1**: 331. 1840, in part; Torr. & Gray, Fl. N. Am. **2**: 436. 1843; Benth. & Hook. f. Gen. Pl. **2**: 446. 1873, in part; Pfeiffer, Nom. Bot. 2^2: 1136. 1874; Hemsl. Biol. Cent.-Am. Bot. **2**: 235. 1881, excl. *Cacalia;* Gray, Syn. Fl. N. Am. 1^2: 383. 1884, and ed. 2, 1888; Hoffmann in Engl. & Prantl,

Nat. Pflanzenf. IV. Abt. 5, 296. 1892, excl. *Emilia;* Greenm. Monogr. Senecio, I. Teil, 1901, and in Engl. Bot. Jahrb. **32**: 1–33. 1902; Dalla Torre & Harms, Gen. Siph. 563. 1900–1907, mainly.

Jacobaea Thunb. Fl. Cap. Prodr. Praef. 1794.

Obaejaca Cass. Dict. Sci. Nat. **35**: 270. 1825.

Roldana LaLlave & Lex. Nov. Veg., fasc. 2, 13. 1825.

Rugelia Schuttlew. in Chapm. Fl. Southern U. S. 246. 1860.

Cacalia, Cineraria, and *Gynoxis,* in part, of authors.

Heads heterogamous and radiate, or discoid. Involucre cylindrical campanulate, occasionally flask-shaped, usually subtended by calyculate bracteoles; bracts of the involucre uniseriate, or by overlapping subbiseriate, variable in number but tending to approach a definite series of numbers, namely 5–8–13–21. Ray-flowers when present disposed in a single row, fertile; rays sometimes more or less reduced. Disk-flowers perfect; corollas slenderly tubular to abruptly ampliated above into a campanulate 5-toothed limb, teeth mostly short. Anthers obtuse or slightly sagittate at the base. Style-branches subterete, recurved-spreading, truncate, rounded-obtuse, occasionally terminated by a small penicillate tuft of hairs, or (in the subgenus *Pseudogynoxis*) terminated by a triangular acute or acuminate appendage. Achenes subterete, usually ribbed, glabrous, or more or less hirtellous especially on the ribs. Pappus of numerous usually white setae.—Annual, biennial, or perennial herbs, shrubs, climbers, or even arboreous plants, with alternate or radical, very variable, pinnately or palmately veined, entire or variously divided leaves.

Synopsis of the Subgenera and Sections

Subgenus I. Eusenecio Hoffm. Style-branches truncate, rounded-obtuse or occasionally terminated by a penicillate tuft of hairs.

A. Stems erect or ascending, not climbing.
  a. Stems not abruptly terminated by a foreshortening of the main axis; oil-tubes not richly developed in the peripheral portion of the stem.
    α. Leaves pinnately veined; lateral nerves not numerous or conspicuous.
      I. Annual herbs ..... § 1. *Annui*

II. Biennial or perennial herbs (rarely annual).
1. Stems herbaceous.
* Heads usually radiate; flowers yellow, except in *S. Greenei* and *S. crocatus*.
† Stem leafy to the inflorescence; leaves laciniately pinnatifid to triternately divided.
0. Native species .....§ 2. *Eremophili*
00. Introduced species ...§ 3. *Jacobaeae*
†† Stem not uniformly leafy to the inflorescence; leaves pinnate or the lower simple and undivided.
0. Leaves pinnate or pinnatisect, rarely undivided .....§ 4. *Sanguisorboidei*
00. Lower leaves rotund-ovate, simple and undivided .....§ 5. *Bolanderiani*
††† Stem not uniformly leafy to the inflorescence; leaves simple and entire to lyrate-pinnatifid; plants either quite glabrous from the start or more or less permanently tomentose; pubescence never of long jointed hairs.
0. Plants glabrous or early glabrate; leaves upwardly reduced on the stem..§ 6. *Aurei*
00. Plants at first tomentose, later glabrate; leaves more uniform throughout and mostly pinnately divided .....§ 7. *Lobati*
000. Plants permanently tomentose or more or less glabrate; stem-leaves upwardly reduced .....§ 8. *Tomentosi*
†††† Stem leafy to the inflorescence (except in § 9); pubescence usually of long jointed hairs.
0. Stem-leaves not amplexicaul.
δ. Leaves not digitately divided ..§ 9. *Columbiani*
δδ. Leaves digitately divided .....§ 10. *Digitati*
00. Stem-leaves amplexicaul.
δ. Involucre ecalyculate .....§ 11. *Cineraroidei*
δδ. Involucre calyculate .....§ 12. *Amplectentes*

** Heads discoid; flowers whitish or purplish.
† Heads 2 cm. or more high; corollas deeply 5-lobed.....§ 13. *Rugeliae*
†† Heads 1 cm. high; corollas shortly 5-toothed .....§ 14. *Mulgedifolii*
2. Stems ligneous at the base.
* Involucre barely calyculate; plants densely white-tomentose throughout .....§ 15. *Incani*
** Involucre calyculate; plants glabrous or pubescent.....§ 16. *Suffruticosi*
3. Shrubs or tree-like plants.....§ 17. *Fruticosi*
β. Leaves palmately veined.....§ 18. *Palmatinerves*
γ. Leaves pinnately veined; lateral nerves parallel-arcuate, numerous and conspicuous..§ 19. *Multinervii*
b. Stems abruptly terminated by a fore-shortening of the main axis and bearing at the top two to several, more or less pedunculate axillary compound corymbose cymes; oil-tubes richly developed in the peripheral portion of the stem..§ 20. *Terminales*
B. Stems climbing .....§ 21. *Streptothamni*

Subgenus II. Pseudogynoxis Greenm. Style-branches terminated by triangular acute or acuminate dorsally hispidulous appendages.....§ 22. *Convolvuloidei*

Subgenus I. Eusenecio Hoffm.

Subgenus I. Eusenecio Hoffm. in Engl. & Prantl, Nat. Pflanzenf. IV. Abt. 5. 297. 1892; Greenm. Monogr. Senecio, I. Teil, 21, 30. 1901, and in Engl. Bot. Jahrb. **32** : 17, 26. 1902.

Annuals, biennials or perennials; stems erect, scandent or climbing; leaves pinnately or palmately veined; heads radiate or discoid; style-branches truncate or rounded-obtuse, not infrequently bearing a penicillate tuft of hairs at the extreme tip. Sect. 1–21.

Sect. 1. Annui Hoffm.

§ 1. Annui Hoffm. in Engl. & Prantl, Nat. Pflanzenf. IV. Abt. 5, 297. 1892; Greenm. Monogr. Senecio, I. Teil, 21, 23. 1901, and in Engl. Bot. Jahrb. **32** : 17, 19. 1902. *Obacjacae* DC. Prodr. **6** : 341. 1837.

Annual herbs; heads radiate or discoid; involucre narrowly campanulate or subcylindric, usually calyculate; achenes pubescent or glabrous. Sp. 1–7.

Key to the Species

A. Heads radiate or discoid; rays when present minute, barely surpassing the involucre.
  a. Plants viscid-pubescent ..... 1. *S. viscosus*
  b. Plants glabrous or pubescent, not viscid.
    α. Leaves coarsely dentate, auriculate-clasping by a broad base ..... 2. *S. mohavensis*
    β. Leaves chiefly pinnatifid, not greatly expanded at the base.
      I. Bracteoles black-tipped, heads discoid ..... 3. *S. vulgaris*
      II. Bracteoles not black-tipped; heads minutely radiate.
        1. Plants slightly pubescent ..... 4. *S. sylvaticus*
        2. Plants glabrous ..... 5. *S. aphanactis*

B. Heads radiate; rays conspicuous, much surpassing the involucre.
  a. Plants glabrous or pubescent, not arachnoid-tomentose.
    α. Leaves thin ..... 6. *S. californicus*
    β. Leaves thickish, succulent ..... 6a. var. *ammophilus*
  b. Plants arachnoid-tomentose ..... 7. *S. ampullaceus*

1. Senecio viscosus L. Sp. Pl. **2** : 868. 1753, and ed. 2, 1217. 1763; Sow. Eng. Bot. *pl. 32*. 1790; Willd. Sp. Pl. **3** : 1984. 1800; Oeder, Fl. Dan. *pl. 1230*. 1799; Schkuhr, Handb. *pl. 267*. 1808; DC. Prodr. **6** : 342. 1837; Gray, Syn. Fl. N. Am. 1^2 : 394. 1884; Greenm. Monogr. Senecio, I. Teil, 23. 1901, in Engl. Bot. Jahrb. **32** : 19. 1902, and in Gray, Manual, ed. 7, 853. 1907; Britton, Manual, ed. 2, 1029. 1905; Britton & Brown, Ill. Fl., ed. 2, **3** : 540. 1913.

Obaejaca viscosa Cass. Dict. Sci. Nat. **35** : 270. 1825.

A strong-scented annual, viscid-pubescent throughout; stem erect, 2 to 4 dm. high, usually branched from the base; leaves sessile, half-clasping, 3 to 6 cm. long, two-thirds as broad, once or twice pinnatifid with angulate-sinuate lobes and rounded sinuses; heads radiate (rarely discoid); rays inconspicuous; achenes glabrous.

Distribution: eastern North America from Nova Scotia to Pennsylvania, near the coast.

Specimens examined:

Nova Scotia: Pictou, 1 Nov., 1874, *Fowler* (Field Mus. Herb.); Pictou Landing, 21 July, 1883, *Macoun 14883* (Geol. Surv. Canada Herb.); Kentville, 22 Aug., 1902, *Fernald* (Gray Herb. and Geol. Surv. Canada Herb.).

New Brunswick: Schediac, 11 Sept., 1874, *Fowler* (Geol.

Surv. Canada Herb. *14882* and Kew Herb. *872,* in part); Painsec Junction, 8 Aug., 1901, *Churchill* (Gray Herb.).

Massachusetts: along Boston and Albany Railroad, Sept., 1879, *Boott* (Gray Herb.); streets of Cambridge, 1 Sept., 1897, *Robinson* (Gray Herb.).

Rhode Island: wharves at Providence, 4 Sept., 1874, *Congdon* (Gray Herb.); streets of Providence, coll. of 1876, *Bailey* (Gray Herb. and Field Mus. Herb.); East Providence, 20 July, 1890, *Collins* (Mo. Bot. Gard. Herb.).

Pennsylvania: on ballast, Girard Point, July, 1877, *Martindale* (Gray Herb.) and Aug., 1877, *Rothrock* (Field Mus. Herb.). Introduced from Europe.

2. S. mohavensis Gray, Syn. Fl. N. Am. 1^2: 446. 1884, and ed. 2, 454. 1886; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902. Plate 17.

Glabrous throughout; stems erect or nearly so, 1.5 to 4 dm. high, freely branching; leaves membranous, ovate to oblong-ovate, 2 to 6 cm. long, 1 to 4 cm. broad, apiculate-acute, irregularly toothed, or somewhat laciniate-dentate, the lowermost narrowed into a petiolate base, those of the stem sessile and amplexicaul; inflorescence a terminal corymbose cyme; heads 1 cm. high on slender peduncles, discoid or with much reduced ligulate flowers; involucre calyculate with few short inconspicuous bracteoles, 18–20-flowered; bracts of the involucre about 13, linear, acute, slightly shorter than the flowers of the disk; achenes canescent pubescent.

Distribution: southern California, Arizona, and northern Mexico.

Specimens examined:

California: Pleasant Cañon, Panamint Mountains, alt. 900 m., 10 May, 1906, *Hall & Chandler 6910* (Mo. Bot. Gard. Herb. and Field Mus. Herb.); Hall Cañon, Panamint Mountains, 18 April, 1891, *Coville & Funston 697* (U. S. Nat. Herb.); Panamint Valley, alt. 450 m., 5 May, 1897, *Jones* (Mo. Bot. Gard. Herb.); Mohave region, April–May, 1884, *Lemmon 3129* (Gray Herb.), TYPE; Colorado Desert, April, 1889, *C. R. Orcutt* (U. S. Nat. Herb. and Gray Herb.).

Arizona: Tempe, 21 April, 1892, *Ganong & Blaschka* (Gray Herb.).

Sonora: near the U. S. boundary line, 28 March, 1884, *Pringle* (Gray Herb. and U. S. Nat. Herb.).

3. **S. vulgaris** L. Sp. Pl. **2**: 867. 1753, ed. 2, 1216. 1763; Fl. Dan. *pl. 513*. 1770; Willd. Sp. Pl. **3**: 1979. 1800; Sow. Eng. Bot. *pl. 747*. 1800; Pursh, Fl. **2**: 528. 1814; DC. Prodr. **6**: 341. 1837; Reichb. Ic. Fl. Germ. & Helv. **16**: 35. *pl. 68* (CMLIX), *fig. I, 1–9*. 1854; Gray, Syn. Fl. N. Am. 1^2: 394. 1886; Greenm. Monogr. Senecio, I. Teil, 23. 1901, in Engl. Bot. Jahrb. **32**: 19. 1902, and in Gray, Manual, ed. 7, 853. 1907; Britton, Manual, ed. 2, 1029. 1905; Britton & Brown, Ill. Fl., ed. 2, **3**: 539. 1913.

Annual, 1 to 4 dm. high, glabrous or subfloccose pubescent especially in the axils of the upper leaves and in the inflorescence; leaves 2 to 8 cm. long, 0.5 to 2.5 cm. broad, more or less lyrately pinnatifid and angulate-toothed, lower leaves narrowed into a margined petiole, the upper sessile and semi-amplexicaul; heads discoid; the rather numerous small calyculate bracteoles as well as the bracts of the involucre usually black-tipped; achenes hirtellous-puberulent along the angles or ribs.

Distribution: Labrador, Newfoundland to North Carolina, west to Alaska, California, and New Mexico. Europe, Asia, and Africa.

Specimens examined:

Labrador: Hopedale, 4–6 Aug., 1897, *Sornborger 162* (Gray Herb.).

Newfoundland: rocky hills, St. John's, 1 Aug., 1894, *Robinson & Schrenk* (Gray Herb., U. S. Nat. Herb., Geol. Surv. Canada Herb., and Mo. Bot. Gard. Herb.); Funk Island, 23 July, 1887, *Palmer* (U. S. Nat. Herb.); rich soil, field near shore, Channel, 27 July–1 Aug., 1901, *Howe & Lang 802* (Gray Herb.); Barred Island, 13 Aug., 1903, *Sornborger* (Gray Herb.).

Nova Scotia: dry soil, roadsides, North Sydney, Cape Breton, 21–25 July, 1901, *Howe & Lang 639* (Gray Herb.);

Boylston, July, 1890, *Hamilton 22848* (Geol. Surv. Canada Herb.); Baddeck, Cape Breton Island, 25 July, 1898, *Macoun 19721* (Geol. Surv. Canada Herb.).

New Brunswick: along railroad, Conners, 22 July, 1908, *Mackenzie 3646* (Mo. Bot. Gard. Herb.); Shediac, 11 Sept., 1874, *Fowler 872* in part. (Kew Herb.).

Quebec: shore of St. Lawrence, Gaspé, Matane Co., *Forbes* (Gray Herb.); Gaspé Basin, 24 July, 1882, *Macoun 14889* (Geol. Surv. Canada Herb.).

Ontario: Ottawa, 20 July, 1891, *Scott 14885* (Geol. Surv. Canada Herb.); Belleville, 10 Aug., 1877, *Macoun 14890* (Geol. Surv. Canada Herb.); northeast of Sarnia, Lambton Co., *Wheatley* (Mo. Bot. Gard. Herb.); Wingham, Aug., 1890, *Morton 14886* (Geol. Surv. Canada Herb.); Kingston, Sept., 1896, *Fowler* (Field Mus. Herb.); Sarnia, 18 June, 1901, *Macoun 26677* (Geol. Surv. Canada Herb.).

Saskatchewan: between Cumberland House and Hudson Bay, *Richardson 14887* (Geol. Surv. Canada Herb.); Prince Albert, 13 July, 1896, *Macoun 12174* (Geol. Surv. Canada Herb.).

Alberta: waste ground, Prince's Island, near Calgary, 21 Aug., 1913, *Moodie 31* (Field Mus. Herb.).

British Columbia: Burrard Inlet, 22 July, 1889, *Macoun* (Gray Herb. and Geol. Surv. Canada Herb.); vicinity of Victoria, 9 April, 1908, *Macoun 78949* (Field Mus. Herb.); along railway embankment, Sicamous, 20 July, 1904, *Macoun 62191* (Geol. Surv. Canada Herb.); Cedar Hill, Vancouver Island, 21 May, 1887, *Macoun 14884* (Geol. Surv. Canada Herb.); near Victoria, 23 May, 1893, collector not indicated, *550* (Geol. Surv. Canada Herb.); Victoria, 10 June, 1875, *Dawson 14888* (Geol. Surv. Canada Herb.).

Alaska: vicinity of Sitka, July, 1891, *Wright 1538* (Mo. Bot. Gard. Herb.); Sitka, July, 1881, *McLean* (U. S. Nat. Herb.); Skagway, 29 July, 1907, *Cowles 889* (Field Mus. Herb. and Mo. Bot. Gard. Herb.).

Maine: Baker's Island, 19 July, 1883, *Redfield* (Mo. Bot. Gard. Herb.).

Vermont: waste ground, Rutland, 1 Sept., 1899, *Eggleston 1383* (Gray Herb.).

Massachusetts: Ipswich, *Oakes* (Gray Herb. and U. S. Nat. Herb.); Nahant, 6 July, 1878, *Kellermann* (Mo. Bot. Gard. Herb.); Revere Beach, 9 July, 1898, *Greenman 515* (Gray Herb.); Cambridge, *Chickering* (U. S. Nat. Herb.); roadsides, West Cambridge, 29 Sept., 1894, local collection (Gray Herb.); Swampscott, 21 June, 1897, *Weatherby* (Gray Herb.); Ipswich, July, 1874, *Morong* (Field Mus. Herb.).

Rhode Island: waste places, Providence, Sept., 1844, *Thurber* (Gray Herb.); Providence, 2 July, 1892, *Collins & Bailey* (U. S. Nat. Herb.); Cat Swamp, Providence, 23 June, 1895, *Collins* (U. S. Nat. Herb.); Providence, 16 Aug., 1873, *Congdon* (Field Mus. Herb.); Providence, July, 1878, *Bailey* (Mo. Bot. Gard. Herb.).

New York: Syracuse, June, 1887, *Overacker* (Mo. Bot. Gard. Herb.); Troy, collector and date not indicated (Gray Herb.); Ithaca, 12 Oct., 1892, *H. von Schrenk* (Mo. Bot. Gard. Herb.); near Fiske mansion, Ithaca, 21 May, 1884 (U. S. Nat. Herb.); Hunter's Point, Long Island, Sept., 1879, *J. Schrenk* (U. S. Nat. Herb.); Elmira City, 28 Aug., 1898, *Lucy* (Field Mus. Herb.); Troy, June, 1873, *Jesup* (Field Mus. Herb.).

Pennsylvania: Girard Point, Philadelphia, Aug., 1877, *Rothrock* (Field Mus. Herb.).

New Jersey: Camden, July, 1876, *Martindale* (U. S. Nat. Herb.); Kaighn's Point, Camden, 16 July, 1865, *Parker* (Mo. Bot. Gard. Herb.).

Maryland: vicinity of Oakland, 5 Sept., 1910, *Steele* (U. S. Nat. Herb.).

District of Columbia: waste ground, Washington, 14 Sept., 1891, *Blanchard* (Mo. Bot. Gard. Herb.); above Uniontown, 27 May, 1883, *Ward* (U. S. Nat. Herb.).

North Carolina: cultivated grounds, Biltmore, 4 May, 1897, *Biltmore Herb. 883*[b] (Gray Herb., Mo. Bot. Gard. Herb., and Field Mus. Herb.).

Ohio: Oberlin, June, 1892 and 1895, *Ricksecker* (U. S. Nat. Herb.).

Michigan: waste ground, Keweenaw Co., July, 1887, *Farwell* (Gray Herb.).

Wisconsin: St. Croix Co., coll. of 1888, *Matthews* (U. S. Nat. Herb.); Preble, 20 May, 1883, *Schuette* (Field Mus. Herb.); Green Bay, 11 July, 1897 and 29 Sept., 1901, *Schuette* (Field Mus. Herb.).

Nebraska: Valley Co., July, 1886, *Webber* (Field Mus. Herb.).

Montana: Willow Creek, 14 June, 1883 *Scribner 123*[c] (Gray Herb.); Columbia Falls, 21 June, 1894, *Williams 965* (Gray Herb. and U. S. Nat. Herb.).

Wyoming: Sundance, 4 July, 1896, *Nelson 2201* (Mo. Bot. Gard. Herb.).

Colorado: valley near Empire, Sept., 1892, *Patterson* (Gray Herb.); along railroad at Georgetown, Aug.–Sept., 1892, *Patterson* (Field Mus. Herb.).

New Mexico: Sante Fe, 14 Sept., 1895, *Mulford 1301* (Mo. Bot. Gard. Herb.); 4 May, 1897, *A. A. & E. G. Heller 3657* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.).

Idaho: frequent in moist places, Julietta, Latah Co., 8 June, 1892, *Sandberg, McDougal & Heller 343* (Gray Herb., Field Mus. Herb., and U. S. Nat. Herb.); waste ground in the Palouse Country and about Lake Coeur d'Alene, June–July, 1892, *Aiton* (Field Mus. Herb. and Mo. Bot. Gard. Herb.).

Washington: on mountains near the lower Cascades, 29 May, 1886, *Suksdorf* (Gray Herb.); Seattle, 6 March, 1889, *Smith* (Mo. Bot. Gard. Herb.); in fields, Pullman, 2 June, 1894, *Piper* (Mo. Bot. Gard. Herb.); Hoquiam, 5 June, 1897, *Lamb 1146* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); San Juan Island, July, 1914, *Reynolds* (Field Mus. Herb.); Index, Snohomish Co., July, 1898, *Savage, Cameron & Lenocker* (Field Mus. Herb.); Granddalles, 3 Sept., 1904, *Westgate 3997* (U. S. Nat. Herb.); Klickitat Co., June, 1878, *Suksdorf* (Gray Herb.).

Oregon: cultivated fields, Sauvie Island, June, 1880, *Howell* (Gray Herb.); Portland, 1 June, 1884, *Henderson 555* (Mo. Bot. Gard. Herb.); Portland, Feb., 1900, *Lunell*, and without date *Sargent* (Gray Herb.); Bonneville, 6 Aug., 1895,

Canby (U. S. Nat Herb.); Catching Inlet, 10 May, 1911, *Smith 3700* (Field Mus. Herb.); Charleston Bay, 6 May, 1911, *Smith 3668* (Field Mus. Herb.); North Slough, 1 March, 1911, *Smith 3487;* Coos Co., 2 March, 1911, *Smith 3494* (Field Mus. Herb.); Portland, March, 1889, *Drake & Dickson* (Field Mus. Herb.); without definite locality, coll. of 1868–69, *Kellogg & Harford 536* (U. S. Nat. Herb.).

California: Oakland, March, 1864, *Bolander 2777* (Gray Herb. and Mo. Bot. Gard. Herb.) and May, 1865, *Bolander 434* (Gray Herb.); without definite locality, coll. of 1880, *Norton* (Mo. Bot. Gard. Herb.); near Mendocino, May, 1898, *Brown 758* (Mo. Bot. Gard. Herb.); Mendocino Co., June, 1898, *Brown 458* (Field Mus. Herb.); Stanford University, 2 March, 1902, *Baker 311* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Russian River, near Trenton, 16 March, 1902, *Heller & Brown 5072* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Big River, Mendocino Co., July, 1903, *McMurphy 374* (U. S. Nat. Herb.); near Saratoga, Santa Clara Co., 25 Feb., 1906, *Pendleton 288* (U. S. Nat. Herb.).

4. S. sylvaticus L. Sp. Pl. **2**: 868. 1753, and ed. 2, 1217. 1763; Sow. Eng. Bot. *pl. 748.* 1800; Willd. Sp. Pl. **3**: 1985. 1800; Fl. Dan. *pl. 869.* 1782; DC. Prodr. **6**: 342. 1837; Gray, Syn. Fl. N. Am. 1^2: 394. 1884; Greenm. Monogr. Senecio, I. Teil, 23. 1901, in Engl. Bot. Jahrb. **32**: 19. 1902, and in Gray, Manual, ed. 7, 853. 1907; Britton, Manual, ed. 2, 1029. 1905; Britton & Brown, Ill. Fl., ed. 2, **3**: 539. 1913.

Obaejaca sylvatica Cass. Dict. Sci. Nat. **35**: 271. 1825.

Stem erect, simple or branched, 1 to 4 dm. or more high, usually somewhat pubescent; leaves more or less pinnatifid with unequal lobes, 2 to 15 cm. long, 1 to 8 cm. broad; the lower leaves petioled, the upper sessile, clasping and auriculate-sagittate; inflorescence naked or nearly so; heads cylindrical, sparingly calyculate, radiate; ligules barely surpassing the involucre, not infrequently much reduced; achenes canescent-pubescent.

Distribution: Newfoundland to Maine, Ohio, and on Pacific coast.

Specimens examined:

Newfoundland: railway ballast, Whitbourne, 17 Aug., 1894, *Robinson & Schrenk* (Gray Herb., U. S. Nat. Herb., Mo. Bot. Gard. Herb., and Geol. Surv. Canada Herb.).

Prince Edward Island: sand dunes, Tracadie Beach, 25 July, 1901, *Churchill* (Gray Herb. and Mo. Bot. Gard. Herb.); waste places, Brackley Point, 28 Aug., 1888; *Macoun 14874* (Geol. Surv. Canada Herb.).

Nova Scotia: clearings and open woods, Sydney, Cape Breton Island, 17 Aug., 1902, *Fernald* (Gray Herb.); Boylston, Aug., 1890, *Hamilton 22847* (Geol. Surv. Canada Herb.); Truro, without date, *Maccullock* (Gray Herb.); Elizabethtown, Cape Breton Island, 2 Aug., 1898, *Macoun 19719* (Gray Herb. and Geol. Surv. Canada Herb.); Baddeck Bay, Cape Breton Island, 11 Aug., 1898, *Macoun 19720* (Gray Herb. and Geol. Surv. Canada Herb.); sea cliffs, Black Hole, near Baxter's Harbor, 24 Aug., 1902, *Fernald* (Gray Herb.); on pebbly beach, Purcell's Cove, Halifax Harbor, 2–6 Sept., 1901, *Howe & Lang 1512* (Gray Herb.); open woods, Starrs Point, Kings Co., 23 Aug., 1902, *Fernald* (Gray Herb.); McNiels Harbor, Cape Breton Island, 4 Aug., 1898, sheet *19722* (Geol. Surv. Canada Herb.).

New Brunswick: Grand Manan, 26 July, 1891, *Churchill* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); Falls of the St. John River, St. John, 22 July, 1902, *Williams & Fernald* (Gray Herb.).

Quebec: beach of Gaspé Bay, Gaspé Co., 24–27 Aug., 1904, *Collins, Fernald & Pease* (Gray Herb.).

British Columbia: Vancouver Island, 6 Aug., 1909, *Macoun 78950* and *78951* (Field Mus. Herb.).

Maine: island in Penobscot Bay, Aug., 1896, *F. L. & L. H. Harvey 554c* (U. S. Nat. Herb.).

Ohio: near Painsville, coll. of 1892, *Hacker 123* (Gray Herb.).

Washington: Seattle, Aug., 1909, *Piper* (U. S. Nat. Herb.); on old burn near farms, Port Crescent, Aug., 1911, *Webster 19* (U. S. Nat. Herb.); old camps, Granite Falls, Snohomish Co., 31 Oct., 1911, *Smith 4226* (Field Mus. Herb.); Iron Mountain,

Granite Falls, alt. 300 m., 28 Oct., 1911, *Smith 4224* (Field Mus. Herb.).

Oregon: region of Coos Bay, 10 Sept., 1911, *House 4848* (U. S. Nat. Herb.).

California: Vance's Camp, Humboldt Co., 5 June, 1911, *Smith 3778* (Field Mus. Herb.); vicinity of Eureka, 20 June, 1907, *J. P. Tracy 2571* (Univ. Calif. Herb. and Mo. Bot. Gard. Herb.).

5. S. aphanactis Greene, Pittonia, **1**: 220. 1888, and Fl. Franciscana 464. 1897; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

S. sylvaticus Gray, Bot. Calif. **1**: 410. 1876, not L.; Jepson, Fl. West. Mid. Calif. 512. 1901.

A slender annual, 1 to 3 dm. high, glabrous or somewhat tomentulose especially in the inflorescence; stem simple or branched; leaves linear to lanceolate, 1 to 4 cm. long, 1 to 12 mm. broad, entire to coarsely dentate or even pinnately lobed, glabrous or nearly so; the lower leaves narrowed into a petiolate base, the upper sessile; inflorescence terminal, few to several-headed; heads somewhat flask-shaped, 6 to 7 mm. high, radiate; involucre sparingly bracteolate, glabrous to tomentulose at the base; rays small, scarcely exceeding the involucre; achenes appressed-canescent.

Distribution: central California, northern Mexico and adjacent islands.

Specimens examined:

California: Mare Island, 30 March, 1874, *Greene* (Gray Herb. and Field Mus. Herb.), CO-TYPE; San Luis Obispo, *Brewer 463* (Gray Herb. and Mo. Bot. Gard. Herb.); San Luis Obispo, coll. of 1886, *Summis* (U. S. Nat. Herb.); Avalon, Santa Catalina Island, March, 1901, *Trask* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); edges of cañons and alkaline flats, San Diego, *Brandegee 3414* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); San Diego, Geological Survey of California 1860–61, *Cooper* (Gray Herb.); North American Pacific coast flora, *Parry 170* (Gray Herb.); San Diego, 5 Feb., 1884, *Orcutt* (Field Mus. Herb.).

Lower California: Cedros Island, April, 1897, *Brandegee* (Gray Herb. and U. S. Nat. Herb.); San Quentin Bay, *Palmer 606* (Kew Herb.).

6. S. californicus DC. Prodr. **6**: 426. 1837; Torr. & Gray, Fl. N. Am. **2**: 437. 1843; Gray, Bot. Calif. **1**: 410. 1876, Syn. Fl. N. Am. 1^2: 393. 1884, and ed. 2, 454. 1886; Greene, Fl. Franciscana, 465. 1897; Greenm. Monogr. Senecio, I. Teil, 23. 1901 and in Engl. Bot. Jahrb. **32**: 19. 1902; Abrams, Fl. Los Angeles and vicinity 439. 1904.

S. californicus var. *laxior* DC. Prodr. **6**: 426. 1837; Torr. & Gray, Fl. N. Am. **2**: 437. 1843.

S. coronopus Nutt. Trans. Am. Phil. Soc. **7**: 413. 1841; Torr. & Gray, Fl. N. Am. **2**: 437. 1843.

An herbaceous glabrous annual; stem erect simple or branched, 1 to 5 dm. high; leaves oblong-spatulate to lanceolate, entire to subpinnatifid, 2.5 to 7 cm. long, .2 to 2 cm. broad, often reddish; the lower leaves often narrowed to a subpetiolate base, the upper sessile and auriculate-clasping at the base; heads radiate, few to several in a loose cyme; bracts of the involucre about 21, often brownish or black-tipped, much exceeded by the yellow conspicuous rays; achenes canescent-pubescent.

Distribution: central California, vicinity of Monterey, south to northern Mexico.

Specimens examined:

California: sand hills, back of Seaside, Monterey Co., 3 April, 1903, *Heller 6509* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Gigling Station, east of Del Monte, in sand, 11 May, 1903, *Heller 6710* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Bardins, Monterey Co., April, 1903, *Elmer 4893* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Del Monte, April, 1902, *Elmer 3576* (Mo. Bot. Gard. Herb.); Arroja Grande, San Luis Obispo Co., 21 Feb., 1886, *Summers* (Gray Herb.); Cuyama, near the boundary between Santa Barbara and San Luis Obispo Counties, 6 May, 1896, *Eastwood* (Gray Herb.); hillsides, Los Angeles Co., 19 March, 1888, *Hasse* (U. S. Nat. Herb.); Los Angeles, May,

1888, *Hasse* (Field Mus. Herb.); copses and grassy slopes, Los Angeles Co., May, 1890, *Hasse* (U. S. Nat. Herb.); Santa Monica, coll. of 1885, *A. Gray* (Gray Herb.); hillsides, Los Angeles Co., Aug., 1890 and June, 1891, *Hasse* (Mo. Bot. Gard. Herb.); "Pueblo los Angeles," *Gambell* (Gray Herb.); without definite locality, *Coulter 335* (Gray Herb.), and coll. of Nov., 1846, *Fremont* (Gray Herb.); Los Angeles, 5 April, 1890, *Fritchey* (Mo. Bot. Gard. Herb.); San Bernardino, *S. B. & W. F. Parish 198* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); San Bernardino, coll. of 1880, *Vasey 330* (Field Mus. Herb., U. S. Nat. Herb., and Gray Herb.); near San Bernardino, May, 1893, *Parish* (Mo. Bot. Gard. Herb.); mesas, San Bernardino Co., May, 1888, *Parish* (Mo. Bot. Gard. Herb.) and April, 1896, *Parish* (Field Mus. Herb.); San Bernardino Co., coll. of 1876, *Parry & Lemmon 206* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); Arrow Head Springs, 15 May, 1891, *Fritchey 18* (Mo. Bot. Gard. Herb.); San Bernardino, *Parish 7* (Gray Herb.); "Cocomurgo," in sandy places, March, 1854, *Bigelow* (Gray Herb.); San Bernardino Co., Feb.–April, 1882, *Parish 233* (Gray Herb.); without definite locality, coll. of 1833, *Douglas 46* (Gray Herb.), CO-TYPE of var. *laxior;* vicinity of Riverside, alt. 600 m., March, 1903, *Hall 3721* (Gray Herb. and Field Mus. Herb.); San Diego, April, 1873, *Bolander & Kellock* (Gray Herb.); San Luis Rey, *Parry* (Gray Herb.); vicinity of Riverside, 26 March, 1907, *Reed 1252* (Field Mus. Herb.); vicinity of San Bernardino, 13 April, 1903, *Parish 5188* (Field Mus. Herb.); without definite locality, *Nuttall* (Gray Herb.); San Diego, April, 1905, *Brandegee* (U. S. Nat. Herb.) and April, 1902, *Brandegee 1647* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); San Diego, April, 1882, *Jones* (U. S. Nat. Herb.); hills, San Diego, 25 April, 1882, *Pringle* (U. S. Nat. Herb. and Field Mus. Herb.); San Diego, 4 May, 1882, *Orcutt 328* (Mo. Bot. Gard. Herb.); Potrero, 6 April, 1889, *Orcutt* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Moro hills, near Fallbrook, 28 April, 1903, *Abrams 3332* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Fallbrook, 27 March, 1882, *Jones 3118* (U. S. Nat. Herb.); San Diego, *Cleveland* (Field

Mus. Herb. and Mo. Bot. Gard. Herb.); San Diego, coll. of June, 1906, *K. Brandegee* (U. S. Nat. Herb.), and coll. of 1875, *Palmer 200* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); side hill, Del Mar, Oct., 1894 and 22 March, 1895, *Angier 14* and *97* (Mo. Bot. Gard. Herb.); Mesa, April, 1895, *Angier* (Field Mus. Herb.); La Jolla, San Diego Co., 17 Feb., 1895, *Snyder* (Field Mus. Herb.); Las Paderes Ranch, San Diego Co., 26 Feb., 1888, *Deane* (Field Mus. Herb.).

Lower California:

Todos Santos Bay, July, 1883, *Orcutt 708* (Gray Herb.); All Saints Bay, May, 1882, *Fish* (Gray Herb.); Punta Bauda, 25 Jan., 1883, *Orcutt 708* (Mo. Bot. Gard. Herb.); Nachoguero Valley, *Schoenfeldt 3401* (U. S. Nat. Herb.).

Var. **ammophilus** (Greene) Greenm. comb. nov.

Senecio ammophilus Greene, Bull. Cal. Acad. **1**: 193. 1886.

Leaves thickish, somewhat succulent, 2 to 4 cm. long, .2 to 1.5 cm. broad, the lower oblanceolate subentire, those of the stem auriculate-clasping, pinnately lobed into oblong or linear obtuse lobes.

Lower California: Cape San Quentin, 10 May, 1885, *Greene* (Gray Herb.), CO-TYPE.

The thick leaves of this variety give the plant a somewhat different appearance from typical forms of the species; but an examination of a large suite of specimens shows numerous transitional forms such as those secured by *Fritchey, Pringle, Bigelow, Palmer 200, Orcutt 708,* and *K. Brandegee.*

7. S. ampullaceus Hook. Bot. Mag. *pl. 3487.* 1836; DC. Prodr. **6**: 428. 1836; Torr. & Gray, Fl. N. Am. **2**: 440. 1843; Engelm. & Gray, Boston Jour. Nat. Hist. **5**: 250. 1845 (Pl. Lindh. **1**: 42. 1845); Gray Syn. Fl. N. Am. 1^2: 393. 1884, and ed. 2, 1886; Coulter, Contr. U. S. Nat. Herb. **2**: 241. 1892; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

S. ampullaceus var. *glaberrimus* Engelm. & Gray, Boston Jour. Nat. Hist. **5**: 250. 1845 (Pl. Lindh. **1**: 42. 1845).

S. ampullaceus var. *floccosus* Engelm. & Gray, Boston Jour. Nat. Hist. **5**: 250. 1845 (Pl. Lindh. **1**: 42. 1845).

Annual, or occasionally becoming biennial, more or less floccose-tomentose throughout, somewhat glabrate; leaves oblong-obovate, acute to lanceolate and acuminate, 5 to 18 cm. long, 1 to 7 cm. broad, entire to coarsely and irregularly dentate; the lower leaves narrowed below into a winged petiole, those of the stem sessile, semiamplexicaul, gradually smaller towards the few to many headed cymose inflorescence; heads 10 to 12 mm. high, radiate, including the rays 1.5 to 3 cm. in diameter; involucre setaceous-calyculate; bracts of the involucre glabrous; achenes pubescent.

Distribution: eastern Texas.

Specimens examined:

Texas: San Felipe, Austin Co., *Drummond* (Kew Herb. and Gray Herb.), TYPE; Corsicana, *Reverchon* (Mo. Bot. Gard. Herb.); near Richland Station, 13 March, 1880, *Joor* (Mo. Bot. Gard. Herb.); Dawson, 16 April, 1903, *Reverchon 3965* and *5965* (Mo. Bot. Gard. Herb.); Llano, May, 1885, *Reverchon 1545* (U. S. Nat. Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); banks of Pecan Bayou, April, 1882, *Reverchon 81* (Gray Herb. and Mo. Bot. Gard. Herb.); sandy soils, Lampasas Co., May, 1884, *Reverchon 1321* (Mo. Bot. Gard. Herb.); Crabapple, Gillespie Co., *Jermy* (Mo. Bot. Gard. Herb.); Hockley, Harris Co., coll. of 1890, *Thurrow* (Field Mus. Herb.); banks of Colorado River, 4 April, 1914, *Young* (Mo. Bot. Gard. Herb. and Univ. of Texas Herb.); on dry ground, Hempstead, 24 April, 1872, *Hall 369* (Gray Herb., U. S. Nat. Herb., and Mo. Bot. Gard Herb.); without locality, coll. of 1848, *Wright* (Gray Herb.); Industry, Austin Co., coll. of 1890, *Wurzlow* (Field Mus. Herb.); banks of railroad near Rosenberg, Fort Bend Co., 13 April, 1900, *Eggert* (Mo. Bot. Gard. Herb.); common on prairies, Columbia, 10 April, 1899, *Bush 95* (Gray Herb. and Mo. Bot. Gard. Herb.); Columbia, 23 April, 1900, *Bush 122* (Mo. Bot. Gard. Herb.); Columbia, 25 March, 1900, *Canby, Sargent & Trelease 153* (U. S. Nat. Herb.); on moist prairie between the Brazos and the Colorado Rivers, April, 1844, *Lindheimer 268, 269* (Mo. Bot. Gard. Herb.), CO-TYPES of var. *glaberrimus* and *floccosus*.

Sect. 2. Eremophili Greenm.

§ 2. Eremophili Greenm. Monogr. Senecio, I. Teil, 21, 23. 1901, and in Engl. Bot. Jahrb. **32** : 17, 19. 1902.

Annual or biennial herbs, not infrequently becoming perennial by the development of a ligneous base; stems leafy; leaves laciniately pinnatifid; inflorescence a terminal corymbose or paniculate cyme; heads radiate, rays conspicuous; achenes glabrous or pubescent. Sp. 8–13.

Key to the Species

A. Plants glabrous; achenes smooth or slightly hirtellous.
  a. Heads 7 to 10 mm. high; involucral bracts 5 to 7 mm. long, usually conspicuously black-tipped.
    α. Involucre 3 to 5 mm. in diameter, 20–35-flowered ..... 8. *S. MacDougalii*
    β. Involucre 5 to 6 mm. in diameter, 35–50-flowered ..... 9. *S. ambrosioides*
  b. Heads 10 to 12 mm. high; involucral bracts 7 to 10 mm. long, not conspicuously black-tipped.
    α. Northern species (Canada and the U. S.) ..... 10. *S. eremophilus*
    β. Southern species (Mexico) ..... 11. *S. Townsendii*

B. Plants more or less tomentose; achenes canescent-pubescent.
  a. Leaves at first tomentulose, later glabrate ..... 12. *S. chihuahuensis*
  b. Leaves permanently tomentulose ..... 13. *S. durangensis*

8. S. MacDougalii Heller, Bull. Torr. Bot. Club **26** : 592. 1899; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902, in part; Rydb. in Fl. Colo. 397. 1906, in part; Wooton & Standley, Contr. U. S. Nat. Herb. **19** : 745. 1915.

S. eremophilus Gray, Syn. Fl. N. Am. **1**^{2} : 392. 1884, and ed. 2, 1886, in part, not Richards.

S. eremophilus var. *attenuatus* Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902.

Glabrous throughout or slightly puberulent above; stem simple or branched, 5 to 8 dm. high, leafy to the inflorescence; leaves more or less laciniately pinnatifid, 3 to 10 cm. long, 1.5 to 5 cm. broad, segments linear to lanceolate, entire to coarsely and unequally dentate; inflorescence terminating the stem and branches in corymbose cymes; heads 7 to 10 mm. high, radiate; involucre narrowly campanulate, calyculate, 3 to 5 mm. in diameter; bracts of the involucre usually 13 (8–13), linear-

lanceolate, 4 to 5 mm. long, commonly black-tipped; ray-flowers 5 to 8, light yellow; disk-flowers 14 to 30; achenes glabrous or slightly puberulent.

Distribution: New Mexico and Arizona.

Specimens examined:

New Mexico: Santa Fe Cañon, Aug., 1880, *Snow* (Mo. Bot. Gard. Herb.); Santa Fe Creek, 9 Sept., 1881, *Engelmann* (Mo. Bot. Gard. Herb.); Santa Fe, 14 Aug., 1895, *Mulford 1292* (Mo. Bot. Gard. Herb.); near Pecos, alt. 2040 m., 25 Aug., 1908, *Standley 5311* (Mo. Bot. Gard. Herb.); Pecos River National Forest, alt. 2560 m., 10 Aug., 1908, *Standley 4873* (U. S. Nat. Herb.); White Mountains, alt. 2130 m., 6 Aug., 1897, *Wooton 290* (Gray Herb. and Mo. Bot. Gard. Herb.); White Mountains, alt. 2255 m., 25 Aug., 1907, *Wooton & Standley 3672* (U. S. Nat. Herb.); head of Bear Creek, coll. of 1903, *Plummer* (U. S. Nat. Herb.); Gilmore's Ranch, White Mountains, alt. 2280 m., 23 Sept., 1906, *Standley* (Mo. Bot. Gard. Herb.); G. O. S. Ranch, Grant Co., 27 Aug.–12 Sept., 1911, *Holzinger* (U. S. Nat. Herb.).

Arizona: Walnut Cañon, alt. 2130 m., *MacDougal 342* (Gray Herb. and Field Mus. Herb.), CO-TYPE; near Flagstaff, May–Oct., 1900, *Purpus* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Mt. Agassiz, alt. 3050 m., 10 Sept., 1909, *Pearson 315* (U. S. Nat. Herb.); Humphrey Peak, July, 1883, *Rusby 337* (Gray Herb. and Field Mus. Herb.); Barfoot Park, Chiricahua Mountains, 24 Oct., 1906, *Blumer 1484* (U. S. Nat. Herb. and Field Mus. Herb.); Huachuca Mountains, Sept., 1882, *Lemmon 2785* (Gray Herb., U. S. Nat. Herb., and Field Mus. Herb.); Huachuca Mountains, 17 Oct., 1903, *Mearns 2581* (U. S. Nat. Herb.).

9. S. ambrosioides Rydb. Bull. Torr. Bot. Club **37**: 467. 1910; Wooton & Standley, Contr. U. S. Nat. Herb. **19**: 745. 1915.

S. eremophilus Gray, Pl. Fendl. 108. 1849, as to plant of Fendler; Pac. Rail. Rept. **4**: 111. 1856, as to plant of Bigelow; Syn. Fl. N. Am. 1^2: 392. 1884, and ed. 2. 1886, in part, not

Richards.; Nelson, in Coulter & Nelson, Manual Cent. Rocky Mountains, 583. 1909, in part, not Richards.

S. MacDougalii Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902, in part, not Heller; Rydb. Fl. Colo. 397. 1906, in part, not Heller.

Herbaceous perennial, glabrous or essentially so throughout; stems one to several from a ligneous base, 3 to 5 dm. high; leaves oblanceolate to ovate-lanceolate in general outline, 3 to 13 cm. long, 1 to 5 cm. wide, more or less laciniately pinnatifid into linear to lanceolate, entire to coarsely and unequally dentate divisions; inflorescence a terminal corymbose cyme; heads usually numerous, 7 to 10 mm. high, radiate; involucre subcampanulate, 5 to 7 mm. in diameter, calyculate; bracts of the involucre usually 13, linear-lanceolate, 5 to 7 mm. long, commonly black-tipped; ray-flowers 5 to 8; disk-flowers 30 to 45; achenes hirtellous-puberulent.

Distribution: Wyoming to New Mexico, Idaho, and Arizona.

Specimens examined:

Wyoming: gravelly banks, Centennial Mountain, Albany Co., 2 Aug., 1902, *Nelson 8773* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); moist ground in open woods, Centennial, 27 July, 1900, *Nelson 7717* (Gray Herb. and Mo. Bot. Gard. Herb.); Bridger Peak, Carbon Co., 22 Aug., 1903, *Goodding 1942* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.).

Colorado: Chamber's Lake, alt. 2895 m., 13 Sept., 1896, *Baker* (Mo. Bot. Gard. Herb.); cañon west of Palmer Lake, alt. 2435 m., 12 Aug., 1896, *Crandall* (Mo. Bot. Gard. Herb.); Steamboat Springs, 20 July, 1903, *Goodding 1617* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Boulder, coll. of 1908, *Pace* (Mo. Bot. Gard. Herb.); Denver, 8 Sept., 1905, *Moffat* (Mo. Bot. Gard. Herb.); Georgetown, 19 Aug., 1895, *Shear 4720* (U. S. Nat. Herb.), coll. of 19 July, 1886, *Trelease,* and coll. of 26 July, 1886, *Letterman* (Mo. Bot. Gard. Herb.); Rocky Mountains, Powell's Colorado Exploring Expedition 1868, *Vasey 337* (Gray Herb.); Golden City, 18 Aug., 1870, *Greene 230* (Gray Herb.); Silver Plume, 21 Aug., 1895, *Shear 4999* (U. S. Nat. Herb.); Manitou, Aug., 1881, *Fritchey 14,* in part, and coll. of 16 Aug., 1884, *Letterman* (Mo. Bot. Gard. Herb.);

Ruxton Park, alt. 2700 m., 21 Aug., 1901, *F. E. & E. S. Clements 152* (Gray Herb., U. S. Nat. Herb., and Mo. Bot. Gard. Herb.); Breckenridge, coll. of 1887, *Bereman* (Mo. Bot. Gard. Herb.); Breckenridge, coll. of 1892, *Wislizenus 1063* (Mo. Bot. Gard. Herb.); Oro City, 23 July, 1873, Hayden's U. S. Geol. Survey, *Coulter,* in part (U. S. Nat. Herb.); Green Mountain Falls, alt. 2560 m., 2 Aug., 1892, *Sheldon 485* (U. S. Nat. Herb.); Hotchkiss, alt. 1585 m., 30 June, 1892, *Cowen 287* (U. S. Nat. Herb.); Oak Creek, Fremont Co., Aug., 1873, *Brandegee 716* (Mo. Bot. Gard. Herb.); Gunnison, 25 July, 1901, alt. 2300 m., *Baker 596* (Gray Herb. and Mo. Bot. Gard. Herb.); vicinity of Mount Carbon, Gunnison Co., alt. 2730–2800 m., 4 July and 10 Aug., 1910, *Eggleston 5835* and *6159* (U. S. Nat. Herb.); Pandora, 10 Aug., 1901, *Baker 748* (Gray Herb. and Mo. Bot. Gard. Herb.); Taylor River, 15 Aug., 1873, Hayden's U. S. Geol. Survey, *Coulter* (U. S. Nat. Herb.); Telluride, alt. 2740–3600 m., Aug., 1894, *Tweedy 354* (U. S. Nat. Herb.); Ute Pass, 2 July, 1896, *Shear 3695* (U. S. Nat. Herb.); near Pagosa Peak, alt. 3050 m., 8 Aug., 1899, *Baker 706* (Gray Herb., U. S. Nat. Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Saguache Creek, Sept., 1873, Wheeler Expedition, *Wolf 1086* (U. S. Nat. Herb.); Parrott City, alt. 2740 m., *Baker, Earle & Tracy 475* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); northeast corner of North Park, 3 Aug., 1874, *Barber* (U. S. Nat. Herb.); Twin Lakes, Wheeler Expedition, 1873, *Wolf & Rothrock 562* (Gray Herb., and Field Mus. Herb.); Rocky Mountains, coll. of 1862, *Hall & Harbour 327* (Gray Herb. and Field Mus. Herb.), also coll. of 1861–62, *Parry 26* (Gray Herb. and Mo. Bot. Gard. Herb.); mouth of Bear Creek Cañon, 23 Aug., 1915, *Drushel & Dougan* (Drushel Herb.); upper Clear Creek Valley, alt. 3050 m., 10 Aug., 1874, *Engelmann* (Mo. Bot. Gard. Herb.); Leadville, 8 July, 1886, *Trelease* (Mo. Bot. Gard. Herb.); Tolland, alt. 2895 m., 29 July, 1913, *Overholts* (Mo. Bot. Gard. Herb.); near Breckenridge, alt. 2950 m., Aug., 1901, *Mackenzie 208* (Mo. Bot. Gard. Herb.); Penn's Gulch, near Sunset, 30 July, 1886, *Letterman* (Mo. Bot. Gard. Herb.).

New Mexico: pine forest, Jicarilla Apache Reservation,

near Dulce, alt. 2150–2470 m., 20 Aug., 1911, *Standley 8183* (U. S. Nat. Herb.); Chama, 8 Sept., 1899, *Baker* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Santa Fe Cañon, 3 Oct., 2380–2850 m., 8 July, 1911, *Standley 6564* (U. S. Nat. Herb.); Navajo Indian Reservation in the Tunitcha Mountains, 8 Aug., 1911, *Standley 7591* (U. S. Nat. Herb.); mountains near Las Vegas, July, 1881, *Vasey* (U. S. Nat. Herb.); Santa Fe Cañon, 7 July, 1897, alt. 2440 m., *A. A. & E. G. Heller 3819* (Gray Herb. and Mo. Bot. Gard. Herb.); Sante Fe Cañon, 3 Oct., 1913, *Rose, Fitch & Parkhurst 17714* (U. S. Nat. Herb.); Canoncinto, Santa Fe Co., coll. of 1879, *Brandegee 12078* (Mo. Bot. Gard. Herb.); creek bottom, Santa Fe, 20 Oct., 1846, *Fendler 475* (Gray Herb. and Mo. Bot. Gard. Herb.); Balsam Park, Sandia Mountains, alt. 2500 m., Aug.–Sept., 1914, *Ellis 281* (Mo. Bot. Gard. Herb.); Pecos River Indian Reservation, 6 Aug., 1898, *Coghill 144* (Mo. Bot. Gard. Herb.); Mineral Creek, Sierra Co., alt. 2130 m., 26 Sept., 1904, *Metcalfe 1415* (U. S. Nat. Herb.); Santa Antonita, Whipple's Exploration 1853–54, *Bigelow* (U. S. Nat. Herb. and Gray Herb.); Organ Mountains, alt. 2130 m., 23 Sept., 1906, *Wooton & Standley* (U. S. Nat. Herb.).

Utah: Big Cottonwood Cañon, Salt Lake Co., alt. 2774 m., 10 Aug., 1905, *Garrett 1591* (U. S. Nat. Herb.); Tate Mine, Marysvale, alt. 2740 m., 22 Aug., 1894, *Jones 5858* (Mo. Bot. Gard. Herb.); Bromide Pass, Henry Mountains, alt. 3050 m., 27 July, 1894, *Jones 5695*^{ad} (U. S. Nat. Herb.); slope of Aquarius Plateau, alt. 2750 m., 2 Aug., 1875, *Ward 499* (U. S. Nat. Herb.).

Arizona: Navajo Indian Reservation, about the north end of the Carrizo Mountains, 29 July, 1911, *Standley 7376* (U. S. Nat. Herb.).

Among the specimens here cited, a few, particularly Parry's 26, Overholts', Mackenzie's 208, and Engelmann's plant from Upper Clear Creek Valley, might be almost equally well referred to the preceding species, *S. MacDougalii*, to which *S. ambrosioides* is very closely related; but in general the latter may be distinguished by the slightly larger and more numer-

ously flowered heads and usually, but not always, less pinnatisect leaves.

10. **S. eremophilus** Richards. in App. Frankl. 1st Journ. 31. 1823; Hook. Fl. Bor. Am. **1** : 334. 1840; Torr. & Gray, Fl. N. Am. **2** : 444. 1843; Eaton, Bot. King Exp. 191. 1871, in part; Gray, Syn. Fl. N. Am. 1^2 : 392. 1884, and ed. 2, 1886; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902; Nelson in Coulter & Nelson, Manual Cent. Rocky Mountains 583. 1909, in part.

S. pembrinensis Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902.

An herbaceous perennial, glabrous or slightly puberulent in the inflorescence; stems erect, 3 to 8 dm. high, striate; leaves more or less laciniately pinnatifid with linear, lanceolate or oblong, entire or coarsely and unequally dentate divisions; the lower leaves petiolate, the upper subsessile; inflorescence terminating the stem in a somewhat leafy corymbose or paniculate cyme; heads rather large, 10 to 12 mm. high, radiate; involucre campanulate conspicuously calyculate; bracts of the involucre usually 13, linear-lanceolate, acute, 7 to 9 mm. long, glabrous, minutely brownish- or black-tipped; ray-flowers 8 to 10; disk-flowers 40 to 60; achenes ribbed, glabrous, or slightly hirtellous-puberulent.

Distribution: northwestern Canada to Nebraska, Colorado, and Utah.

Specimens examined:

Saskatchewan: Lipton, 11 Aug., 1911, *Clokey 1844* (Mo. Bot. Gard. Herb.); Qu'Appelle River, Assiniboia, Aug., 1883, *Macoun 14839* (Geol. Surv. Canada Herb. and U. S. Nat. Herb.); near Prince Albert, 10 July, 1896, *Macoun 12171* (Geol. Surv. Canada Herb.); in damp thickets north of Saskatchewan River, 22 Aug., 1872, *Macoun 14841* (Geol. Surv. Canada Herb.); Saskatchewan Plains, *Macoun 868* (Kew Herb.).

Alberta: "on gravelly banks of Cedar Lake, Lat. 54°," *Richardson* (Kew Herb.), TYPE; Pembina, coll. of 1873, *Coues* (Gray Herb.); on damp banks, Bow River at Morley, 6 Sept.,

1879, *Macoun 14840* (Geol. Surv. Canada Herb.); Dunvegan, Peace River, 17 Aug., 1879, *Dawson 26686* (Geol. Surv. Canada Herb.); Athabasca Plains, 14 Sept., 1872, *Macoun 1040* (Gray Herb. and Kew Herb.).

South Dakota: Sylvan Lake, 27 Aug., 1897, *Griffiths* (Mo. Bot. Gard. Herb.).

Nebraska: mountain range, south of White Clay Creek, 23 Aug., 1859, Lieut. F. T. Bryan's Expedition, 1856, *H. Engelmann* (Mo. Bot. Gard. Herb.).

Wyoming: on the summits of Big Horn Mountains, Aug., 1859, Reynolds' Expedition to the headwaters of the Missouri and Yellowstone Rivers, *Hayden* (Mo. Bot. Gard. Herb.); Laramie Mountains, *Hayden* (Gray Herb. and Mo. Bot. Gard. Herb.); Laramie Mountains, 17 Aug., 1899, *Schuehut* (U. S. Nat. Herb.).

Colorado: Cascade Cañon, July, 1880, *Eurney* (Mo. Bot. Gard. Herb.); Rocky Mountains, *Hall & Harbour 327,* in part (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Pike's Peak, alt. 3050 m., 25 Aug., 1915, *Drushel & Dougan* (Drushel Herb.); Manitou, Aug., 1881, *Fritchey 14* in part (Mo. Bot. Gard. Herb.), form.

var. **Kingii** (Rydb.) Greenm. comb. nov.

Senecio Kingii Rydb. Bull. Torr. Bot. Club **37**: 468. 1910.

S. eremophilus Eaton, Bot. King Exp. 191. 1871, as to plant of Watson.

S. Watsoni Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

Leaves oblanceolate to oblong-lanceolate, coarsely dentate to pinnatisect with relatively broad divisions; but through several specimens connecting directly with the above species.

Specimen examined:

Utah: Cottonwood Cañon, alt. 2590 m., Aug., 1869, *Watson 676* (Columbia Univ. Herb. and Gray Herb.), TYPE.

11. S. Townsendii Greenm.[1]

Herbaceous perennial, glabrous throughout; stem 6 to 10 dm. high, striate, often purplish; leaves coarsely, unequally

[1] **Senecio Townsendii** Greenm. sp. nov., herbaceus perennis ubique glabrus; caule 6–10 dm. alto, striato saepe purpurascenti; foliis inaequaliter et remote

and remotely dentate to laciniately pinnatifid, oblanceolate to oblong-lanceolate in general outline, 3 to 10 cm. long, 1 to 4 cm. broad, divisions linear and entire to dentate, acute or obtuse; lower leaves petiolate, the upper sessile; inflorescence a loose several to many-headed corymbose cyme; heads 10 to 13 mm. high, radiate; involucre narrowly campanulate, calyculate, glabrous; bracts of the involucre commonly 13, linear-lanceolate, 8 to 10 mm. long, terminated by a small black or brownish penicillate tip; flowers pale yellow; ray-flowers 5 to 8, occasionally much reduced; disk-flowers 35 to 50; achenes glabrous.

Distribution: northern Mexico.

Chihuahua: near Colonia San Garcia in the Sierra Madre, alt. 2285 m., 9 Sept., 1899, *Townsend & Barber 317* (Mo. Bot. Gard. Herb., Gray Herb., and U. S. Nat. Herb.), TYPE; Mound Valley, Sierra Madre Mountains, alt. 2130 m., 18 Sept., 1903, *Jones* (U. S. Nat. Herb.).

The Townsend and Barber specimens have been distributed as "*Senecio Chihuahuanus* Wats." and the Jones plant was distributed as "*Senecio eremophilus*" under which names they may be looked for in herbaria.

12. S. chihuahuensis Watson, Proc. Am. Acad. **23**: 280. 1888; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

An herbacous perennial; stem erect, 4 to 5 dm. high from a rather slender rootstock, striate-angulate, somewhat purplish; early leaves oblanceolate, 3 to 5 cm. long, 1 cm. broad, laciniately dentate, arachnoid-tomentulose on both surfaces; later stem-leaves short-petiolate, or subsessile, oblong-ovate in general outline, about 8 cm. long, one-half to two-thirds as

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grosse-dentatis vel laciniato-pinnatis, oblanceolatis vel oblongo-lanceolatis in circumscriptione, 3–10 cm. longis, 1–4 cm. latis; laciniis linearibus et integris vel dentatis acutis vel obtusis; foliis inferioribus petiolatis, superioribus sessilibus; inflorescentibus laxe corymboso-cymosis multicapitatis; capitulis 10–13 mm. altis, radiatis; involucris anguste campanulatis calyculatis glabris; bracteis involucri 13 lineari-lanceolatis 8–10 mm. longis minute atro- vel fulvo-penicillatis; floribus pallide aurantiabus; floribus femineis 5–8 nonnunquam multo reductis; floribus disci 35–50; achaeniis striatis glabris.—Near Colonia San Garcia in the Sierra Madre, State of Chihuahua, Mexico, alt. 2285 m., 9 Sept., 1899, *Townsend & Barber 317* (Mo. Bot. Gard. Herb., Gray Herb., and U. S. Nat. Herb.), TYPE; Mound Valley, Sierra Madre Mountains, alt. 2135 m., 18 Sept., 1903, *Jones* (U. S. Nat. Herb.).

broad, subbipinnate, at first tomentulose, later becoming glabrous or essentially so, divisions narrow, unequal, cartilaginous-apiculate; inflorescence a terminal corymbose cyme; heads 10 to 12 mm. high, radiate; involucre cylindric-campanulate, calyculate with short linear subulate bracteoles; bracts of the involucre 7 to 9 mm. long, brownish- or black-tipped, shorter than the numerous flowers of the disk; ray-flowers about 8; achenes canescent-pubescent.

Distribution: northern Mexico.

Specimens examined:

Chihuahua: ledges of the Sierra Madre, alt. 2955 m., 7 Oct., 1887, *Pringle 1318* (Gray Herb., Kew Herb., and Mo. Bot. Gard. Herb.), TYPE.

13. S. durangensis Greenm. Field Col. Mus. Bot. Ser. **2**: 275. 1907. Plate 18.

S. ctenophyllus Greenm. Proc. Am. Acad. **43**: 20. 1907, not Phil.

An herbaceous annual, or becoming perennial by the development of a ligneous base; stem simple or branched, erect, 3 to 4 dm. high, arachnoid-tomentose; leaves lanceolate, 2 to 9 cm. long, 1 to 2.5 cm. wide, more or less pinnately divided, permanently arachnoid-tomentulose on both surfaces, lower leaves petiolate, upper sessile; inflorescence a terminal tomentulose corymbose cyme; heads numerous, 8 to 10 mm. high, radiate, calyculate; involucre campanulate, glabrous or nearly so; bracts of the involucre 13, linear-lanceolate, 5 to 6 mm. long, minutely black-tipped, penicillate; ray-flowers 5 to 8, ligules pale yellow; disk-flowers 20 to 30; achenes canous-hirtellous.

Distribution: northern Mexico.

Specimen examined:

Durango: barranca, below Sandia Station, alt. 2135 m., 15 Oct., 1905, *Pringle 10105* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.), TYPE.

SECT. 3. JACOBAEAE DC.

§ 3. JACOBAEAE DC. Prodr. **6**: 348. 1837; Hoffm. in Engl. & Prantl, Nat. Pflanzenf. IV, Abt. 5, 297. 1892; Greenm.

Monogr. Senecio, I. Teil, 21, 23. 1901, and in Engl. Bot. Jahrb. **32** : 17, 19. 1902.

Biennial or perennial herbs with lyrate or 2–3-pinnatisect leaves and radiate heads. Sp. 14–16.

Key to the Species

A. Stem and leaves glabrous or nearly so; involucral bracts narrow, about 1 mm. broad; bracteoles usually black-tipped..... *14. S. rupestris*

B. Stems and leaves more or less permanently floccose-tomentulose; involucral bracts 1.5 to 2 mm. broad; bracteoles not black-tipped.

a. Upper stem-leaves once pinnate..... *15. S. erucifolius*

b. Upper stem-leaves 2–3-pinnatisect..... *16. S. Jacobaea*

14. S. rupestris Waldst. & Kit. Descr. et Ic. Pl. Rar. Hung. **2** : 136. *pl. 128.* 1805; Reichb. Ic. Crit. **4** : 28. *pl. 334. fig. 514.* 1826; Strobl, Fl. Admont. **1**: 57. 1881, and in Flora **65**: 478, 479. 1882; von Hayek, Fl. Stierm. **2** : 564. 1913.

S. laciniatus Bert. in Desv. Jour. Bot. **2**: 76. 1813; Amoen. Ital. 102, 408. 1819.

Senecio nebrodensis var. *glabratus* DC. Prodr. **6** : 350. 1837.

Annual or biennial, sometimes becoming perennial, glabrous throughout or slightly pubescent; stem erect, 3 to 6 dm. high, simple or branched, striate; leaves lanceolate to obovate-lanceolate in general outline, 3 to 10 cm. long, 1 to 4 cm. broad, laciniately lobed or subpinnatiscent, thin in texture, the lobes again sharply dentate; the lower leaves narrowed into a subpetiolate base, the upper sessile and semiamplexicaul; inflorescence a terminal corymbose cyme; heads 8 to 10 mm. high, radiate; involucre calyculate with black-tipped bracteoles; bracts of the involucre about 21, linear-lanceolate, acute, 6 to 7 mm. long; ray-flowers about 13; disk-flowers numerous; achenes glabrous or slightly hirtellous.

Distribution: on ballast near Philadelphia. Introduced from Europe.

Specimen examined:

Pennsylvania: on ballast, Philadelphia, July, 1880, *Martindale* (Gray Herb.).

15. S. erucifolius L. Fl. Suecica, ed. 2, 291. 1755; Huds. Fl. Ang. 366. 1798; DC. Prodr. **6** : 351. 1837; Reichb. Ic. Fl.

Germ. & Helv. **16**: 38. *pl. 75* (CMLXVI). *fig. 1.* 1854; Cosson & Saint-Pierre, Fl. Paris, ed. 10, 518. 1861. Beck von Mannagetta, Fl. Nieder-Oesterr. 1221. 1893.

An herbaceous biennial or perennial, more or less floccose-tomentulose throughout and on the stem and lower leaf-surface often intermixed with hirsute hairs; stems erect, 3 to 10 dm. high, simple or branched; leaves lyrately pinnatifid to pinnatisect, 2 to 10 cm. long, 1 to 6 cm. broad, the lobes subentire, blunt, and submucronate to sharply dentate; lowermost leaves narrowed into a subpetiolate base, the upper sessile and semiamplexicaul; inflorescence a terminal few- to many-headed corymbose cyme; heads about 1 cm. high, radiate; involucre campanulate, calyculate; bracts of the involucre usually 13, lanceolate-oblong, 4 to 5 mm. long, glabrous or slightly floccose-tomentulose, with rather broad scarious margins; ray-flowers about 13; disk-flowers numerous, 50 to 60; achenes hirtellous.

Distribution: on ballast near Philadelphia. Introduced from Europe.

Specimens examined:

Pennsylvania: on ballast, Philadelphia, 30 Aug., 1879, *Parker* (Gray Herb.).

New Jersey: on ballast, Kaighn's Point, *Burk* (Field Mus. Herb.).

16. S. Jacobaea L. Sp. Pl. **2**: 870. 1753; Willd. Sp. Pl. **3**: 1997. 1800; DC. Prodr. **6**: 350. 1837; Sm. & Sow. Eng. Bot. **16**: *pl. 1130.* 1803; Schkuhr, Handb. *pl. 267.* 1808; Reichb. Ic. Fl. Germ. & Helv. **16**: 38. *pl. 73* (CMLXIV). *figs. II. 3, 4.* 1854; Gray, Syn. Fl. N. Am. 1^2: 383. 1884, and ed. 2, 1886; Britton, Manual, ed. 2, 1029. 1905; Gray, Manual, ed. 7, 853. 1907; Britton & Brown, Ill. Fl., ed. 2, **3**: 542. 1913.

Jacobaea vulgaris Vahl in Fl. Dan. **6**: *pl. 944.* 1787; Gaertn. Fruct. **2**: 445. *pl. 170. fig. 1.* 1791. An erect, biennial or perennial herb, 3 dm. or more high, at first usually arachnoid-tomentulose, more or less glabrate; basal leaves petiolate, somewhat lyrate; stem leaves sessile, semiamplexicaul, ovate-oblong in general outline, 3 to 15 cm. long, 1.5 to 7 cm.

broad, 2–3-pinnatisect; inflorescence a terminal corymbose cyme; heads numerous, radiate; achenes pubescent.

Distribution: Newfoundland to New Jersey, occurring along roadsides, in pastures, and on ballast. Introduced from Europe.

Specimens examined:

Newfoundland: roadsides, St. John's, 7–19 Aug., *Robinson & Schrenk* (Gray Herb., U. S. Nat. Herb., Geol. Surv. Canada Herb., and Mo. Bot. Gard. Herb.).

Nova Scotia: L'Ardoire, Cape Breton Island, Aug., 1892, *Faxon* (Gray Herb.); Sydney and Mira Bay, Cape Breton Island, 17 Aug., 1898, *Macoun 19723* (Geol. Surv. Canada Herb.); eastern Nova Scotia, 16 Aug., 1890, *Chickering* (U. S. Nat. Herb.); Boylston, *Hamilton 22844* (Geol. Surv. Canada Herb.); Pictou, 1 Nov., 1874, *Fowler* (Field Mus. Herb.); Pictou Landing, 24 July, 1883, *Macoun 14859* (Geol. Surv. Canada Herb.); pasture, Windsor Junction, 11 July, 1901, *Howe & Lang 427* (Gray Herb.); pasture, near Pictou, 12–18 July, 1901, *Howe & Lang 540* (Gray Herb.).

Prince Edward Island: Tignish, 26 July, 1888, *Macoun, 14858* (Geol. Surv. Canada Herb.); Tracadie Beach, 27 July, 1901, *Churchill* (Gray Herb. and Mo. Bot. Gard. Herb.).

New Brunswick: Miramichi, *Fowler* (Gray Herb. and U. S. Nat. Herb.); near railroad station, Anagance, 19 July, 1901, *Churchill* (Gray Herb. and Mo. Bot. Gard. Herb.).

Quebec: on ballast-filling about fish houses, York, Gaspé Co., 25 Aug., 1904, *Collins, Fernald & Pease* (Gray Herb.).

Ontario: Burlington, 23 Aug., 1883, *Burgess 14857* (Geol. Surv. Canada Herb.).

Pennsylvania: on ballast, July, 1876, *Martindale* (Mo. Bot. Gard. Herb.).

New Jersey: on ballast, Camden, coll. of 1878, *Martindale* (Gray Herb., U. S. Nat. Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); on ballast, Kaighn's Point, *Burk* (Field Mus. Herb.).

Sect. 4. Sanguisorboidei Greenm.

§ 4. Sanguisorboidei Greenm. Monogr. Senecio, I. Teil, 22,

23, 1901, and in Engl. Bot. Jahrb. **32** : 18, 19. 1902. *Lobati* Rydb. Bull. Torr. Bot. Club **27** : 169. 1900, in part.

Annuals, biennials, or perennials, often forming merely a rosette of leaves during the first year; stems erect, 1.5 to 10 dm. high from a distinctly annual root or from a rather stout rootstock; leaves once, twice, or thrice pinnately divided; heads numerous; achenes glabrous or pubescent. Sp. 17–29.

Key to the Species

A. Annuals or biennials.
  a. Bracts of the involucre usually 13, linear-lanceolate, 1 to 2.5 mm. broad ..... *17. S. sanguisorboides*
  b. Bracts of the involucre usually 21, linear or linear-lanceolate, 0.5 to 1.5 mm. broad.
    α. Lateral leaf-segments not abruptly contracted into a narrow base.
      I. Plants of southeastern United States..*18. S. glabellus*
      II. Plants of southwestern Texas and northern Mexico..... *19. S. Greggii*
    β. Lateral leaf-segments abruptly contracted into a narrow base.....*20. S. imparipinnatus*
B. Perennials; upright stem from a horizontal, ascending or suberect rootstock.
  a. Leaves 2–3-pinnatisect; segments narrow.....*21. S. Millefolium*
  b. Leaves once pinnate; segments narrowly obovate to subreniform.
    α. Heads numerous, small, 5 to 10 mm. high.
      I. Involucral bracts usually 21.
        1. Leaves glabrous; achenes hirtellous.*22. S. tampicanus*
        2. Leaves pubescent beneath; achenes glabrous.....*23. S. hypotrichus*
      II. Involucral bracts usually 13.
        1. Lateral leaf-divisions longer than broad.
          * Midrib glabrous ..... *24. S. Sanguisorbae*
          ** Midrib floccose-tomentulose.... *25. S. pinnatisectus*
        2. Lateral leaf-divisions as broad as long .....*26. S. coahuilensis*
    β. Heads fewer and larger, 10 to 14 mm. high.
      I. Leaves pinnately divided nearly to the midrib.
        1. Leaf-divisions few, cuneate to reniform ..... *27. S. leonensis*
        2. Leaf-divisions many, cuneate to linear ..... *28. S. montereyana*
      II. Leaves pinnately divided slightly more than half-way from margin to midrib ..... *29. S. zimapanicus*

17. S. sanguisorboides Rydb. Bull. Torr. Bot. Club **27** : 170. 1900; Wooton & Standley, Contr. U. S. Nat. Herb. **19** : 745. 1915.

Annual or biennial, glabrous or slightly white tomentulose in the axils of the leaves; stem 1.5 to 5 dm. high, striate; leaves usually pinnately divided into cuneate to reniform dentate or crenate-dentate divisions, the terminal division ovate-reniform, 1 to 5 cm. broad; basal and lower stem-leaves petiolate and occasionally undivided; upper stem-leaves sessile and amplexicaul; inflorescence a terminal few to several-headed corymbose cyme; heads radiate; involucre campanulate, barely calyculate; bracts of the involucre usually 13 (rarely 16), lanceolate, 6 to 6.5 mm. long, glabrous; ray-flowers 8 to 10; disk-flowers 30 to 50; achenes ribbed, glabrous.

Distribution: mountains of New Mexico.

Specimens examined:

New Mexico: Willow Gulch, Colfax Co., alt. 3050 m., Aug., 1896, *St. John 115* (Gray Herb.); Santa Fe Cañon, 7 July, 1897, alt. 2440 m., *A. A. & E. G. Heller 3820* (Mo. Bot. Gard. Herb.), CO-TYPE; Santa Fe Creek, 22 June, 1847, *Fendler 438* (Mo. Bot. Gard. Herb.); White Mountains, Lincoln Co., alt. 3048 m., 16 Aug., 1897, *Wooton 494* (Mo. Bot. Gard. Herb.); mouth of Pouchuelo Creek, Pecos River National Forest, alt. 2590 m., 30 June, 1908, *Standley 4093* (Mo. Bot. Gard. Herb.); mouth of Mora River, Pecos River National Forest, alt. 2470 m., 7 July, 1908, *Standley 4250* (Mo. Bot. Gard. Herb.); Pecos River Indian Reservation, 17 July, 1898, *Coghill 71* (Mo. Bot. Gard. Herb.).

18. S. glabellus Poir. Dict. **7**: 102. 1806; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902; Gray, Manual, 853, ed. 7, 1907; Britton & Brown, Ill. Fl. **3**: 540, ed. 2, 1913.

S. lyratus Michx. Fl. Bor. Am. **2**: 120. 1803, not L.

S. lobatus Pers. Syn. **2**: 436. 1807; Nutt. Gen. **2**: 165. 1818; Elliot, Sk. **2**: 332. 1824; Torr. & Gray, Fl. N. Am. **2**: 437. 1843; Gray, Syn. Fl. N. Am. 1^2: 394. 1884, and ed. 2, 1886, mainly; Chapman, Fl. Southern U. S. 266, ed. 3, 1897; Britton & Brown, Ill. Fl. **3**: 481, ed. 1, 1898; Small, Fl. Southeastern U. S.. 1303. 1903, and ed. 2, 1913; Mohr, Contr. U. S. Nat. Herb. **6**: 815. 1901.

S. carolinianus Spreng. Syst. **3** : 559. 1826.

S. densiflorus Martens, Bull. Acad. Roy. Soc. Brux. **8** : 66. 1841.

S. Schweinitzianus Nutt. Trans. Am. Phil. Soc. **7** : 413. 1841.

Annual or biennial, glabrous or slightly tomentulose in the axils of the leaves; stems erect 1 to 10 dm. high, striate; radical leaves petiolate, lyrate, occasionally undivided; those of the stem petiolate or sessile and semiamplexicaul, pinnately divided into rather remote, narrowly cuneate to subreniform unequal divisions; inflorescence a terminal corymbose cyme; heads 6 to 8 mm. high, radiate; ray-flowers 8 to 12; disk-flowers about 50; achenes usually hirtellous-puberulent.

Distribution: North Carolina west to Illinois, Missouri, and South Dakota, south to Florida and eastern Texas. Common on river bottoms and flood-plains.

Specimens examined:

North Carolina: near Wilmington, April, 1888, *McCarthy* (U. S. Nat. Herb.); without locality, *Curtis* (Gray Herb.).

South Carolina: Goose Creek, 19 May, 1885, *A. C. & F. W. Maier* (Gray Herb.); swamps, Summerville, April, 1890, *Taylor* (Field Mus. Herb.).

Georgia: Macon, coll. of 1875, *Curtiss* (U. S. Nat. Herb.); central Georgia, coll. of 1846, *Porter* (Gray Herb.); Butler Island, McIntosh Co., 27 May, 1909, *Smith 2185* (Field Mus. Herb.).

Florida: without locality, *Chapman* (Gray Herb., U. S. Nat. Herb., and Kew Herb.); Fort Orange, 10 April, 1895, *Straub 103* (Gray Herb.); near Chattahooche, *Curtis 1565* (Gray Herb., U. S. Nat. Herb., Kew Herb., and Field Mus. Herb.); River Junction, 19 April, 1898, *Curtis 6370* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Sand Point, 8 April, 1874, *Palmer 301* (Gray Herb., U. S. Nat. Herb., and Mo. Bot. Gard. Herb.); near St. Marks, coll. of 1843, *Rugel* (Mo. Bot. Gard. Herb., and Kew Herb.); Losman's Key, May, 1891, *Simpson 154* (U. S. Nat. Herb. and Field Mus. Herb.); New

Smyrna, *Burgess 563* (Field Mus. Herb.); Gulf Hammock, April, 1876, *Garber* (Field Mus. Herb.).

Illinois: in a damp meadow near Peoria, coll. of 1903, *McDonald* (Field Mus. Herb.); river bottom opposite Decatur, April, 1864, *Stewart* (Field Mus. Herb.); Eldred, Green Co., 9 May, 1891, *Andrews* (Mo. Bot. Gard. Herb.); opposite St. Louis, July, 1839, and May, 1845, *Engelmann* (Mo. Bot. Gard. Herb. and Kew Herb.); Mississippi Valley, St. Clair Co., colls. of 1874, 1875, and 1879, *Eggert* (Mo. Bot. Gard. Herb.); near Falling Spring, 1 June, 1890, *Glatfelter* (Mo. Bot. Gard. Herb.); East St. Louis, 11 June, 1890, *Hitchcock* (Mo. Bot. Gard. Herb.).

Kentucky: Muhlenberg, 5 June, 1901, *Price* (Mo. Bot. Gard. Herb.); without locality, *Short* (Kew Herb.).

Tennessee: in swamps, Rutherford Co., July, 1892, *Bain* (U. S. Nat. Herb.).

Alabama: Tuscaloosa, April, 1892, *Ward* (U. S. Nat. Herb.); Greensboro, coll. of 1857, *Watson* (Gray Herb.); Auburn, Lee Co., 9 April, 1898, *Earle & Baker* (Field Mus. Herb.).

Mississippi: damp fields, North Carrollton, 21 April, 1899, *Clute 24* (Field Mus. Herb.); without locality, coll. of 1843, *Holton* (Kew Herb.).

South Dakota: Fort Pierre, July, 1853, *Hayden* (Mo. Bot. Gard. Herb.).

Missouri: Courtney, 15 May, 1896, *Bush 701* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); vicinity of St. Louis, coll. of about 1840, *Duerinck* (Mo. Bot. Gard. Herb.); Creve Coeur Lake, 8 May, 1859, *Glatfelter* (Mo. Bot. Gard. Herb.); near St. Louis, *Hus 4007* (Mo. Bot. Gard. Herb.); St. Louis Co., 24 May, 1896, *Shannon 250* (Mo. Bot. Gard. Herb.); St. Louis Co., 20 May, 1879, *Eggert* (Mo. Bot. Gard. Herb.); Jefferson Barracks, 6 May, 1890, *Hitchcock* (Mo. Bot. Gard. Herb.); Jefferson Co., 5 May, 1896, *Eggert* (Mo. Bot. Gard. Herb.); Kimmswick, 20 May, 1860, *Engelmann* (Mo. Bot. Gard. Herb.); Kimmswick, 23 May, 1885, *Wislizenus* (Mo. Bot. Gard. Herb.); Sulphur Springs, 14 Aug., 1910, *Sherff 1062* (Field Mus. Herb.); Osage, 13 May, 1901, *Norton* (Mo. Bot. Gard. Herb.);

Batesville, Butler Co., 21 May, 1908, *Smith 534* (Field Mus. Herb.); St. Louis, coll. of 1832, *Drummond* (Kew Herb.); St. Louis, *Riehl 382* (Kew Herb.).

Arkansas: Fulton, 17 April, 1905, *Bush 2354* (Mo. Bot. Gard. Herb.); Fulton, 24 April, 1914, *Palmer 5381* (Mo. Bot. Gard. Herb.); Arkansas Post, 20 March, 1909, *Kellogg* (Mo. Bot. Gard. Herb.); Little Rock, 22 April, 1909, *McNair* (U. S. Nat. Herb.); Little Rock, June, 1886, *Hasse* (Field Mus. Herb.).

Louisiana: without locality, *Hale* (Gray Herb. and Kew Herb.); Gretna, 28 April, 1899, *Ball 315* (Gray Herb., U. S. Nat. Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); between New Orleans and Balize, May, 1829, *Berlandier 556, 1946* (Gray Herb. and Mo. Bot. Gard. Herb.); Balize, April, 1839, *Lindheimer* (Mo. Bot. Gard. Herb.); Baton Rouge, 22 Jan., 1874, *Joor* (Mo. Bot. Gard. Herb.); Holly Ridge, West Carroll Parish, July, 1910, *Mosely* (Field Mus. Herb.); swampy woods, Natchitoches, 16 April, 1915, *Palmer 7253* (Mo. Bot. Gard. Herb.); New Orleans, *Drummond 176, 626* (Kew Herb.); New Orleans, coll. of 26 March, 1847, *Bromfield* (Kew Herb.).

Texas: low ground, San Augustine, 31 March, 1915, *Palmer 7114* (Mo. Bot. Gard. Herb.).

Forma **robustior**, forma nova.

Stout herb; upper stem-leaves 1.5 to 2 dm. long, 8 to 10 cm. wide; the large lateral obovate leaf-lobes alternating with smaller wedge-shaped divisions of the leaf.

Georgia: ditch banks, near Savannah, 21 March, 1882, *J. D. Smith* (Gray Herb.), TYPE. This plant appears to be a giant form with rather marked foliage.

19. S. Greggii Rydb. Bull. Torr. Bot. Club **27**: 170. 1900.

S. tampicanus Gray, Pl. Fendl. 109. 1849 (in Mem. Am. Acad. N. S. **4**), not DC.

S. lobatus Gray, Pl. Wright., part 2, 99. 1853 (in Smithson. Contr. **5**), not Pers.

Annual or biennial, glabrous or with a slight tomentum in the leaf-axils and on the upper side of the leaf along the mid-

rib; stems one to several from a common base, 1.5 to 4 dm. high, striate; leaves lyrate to pinnately divided into cuneate to subrotund divisions; inflorescence a terminal corymbose cyme; heads 5 to 8 mm. high, radiate; involucre campanulate, slightly calyculate; bracts of the involucre about 21, linear-lanceolate, 3 to 5 mm. long, glabrous; ray-flowers 8 to 12; disk-flowers 45 to 60; achenes hispidulous.

Distribution: southern New Mexico, western Texas, and northern Mexico.

Specimens examined:

New Mexico: banks of the Rio Grande near El Paso, *Wright 1413* (Gray Herb.).

Texas: valley of the Rio Grande, below Doñana, Mexican Boundary Survey, *Parry 659* (U. S. Nat. Herb.); El Paso, May, 1881, *Vasey* (U. S. Nat. Herb.); southeastern Texas, Sept., 1879 to Oct., 1880, *Palmer 754* (Gray Herb.).

Chihuahua: valley of Rio Parral, near Santa Rosalia, 21 April, 1847, *Gregg 11,* (Gray Herb.) CO-TYPE; valley near Ortiz, 11 April, 1887, *Pringle* (Field Mus. Herb.).

20. S. imparipinnatus Klatt, Natur. Gesell. Halle **15** : 333. 1881; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902.

S. lobatus Gray, Syn. Fl. N. Am. 1^2 : 394. 1884, and ed. 2. 1886, in part, not Pers.; Coulter, Contr. U. S. Nat. Herb. **2**: 241. 1892, in part, not Pers.

Annual or biennial, glabrous or slightly floccose-tomentulose in the axils of the leaves; stems slender, 1.5 to 4 dm. high, simple or branched from the base; leaves 2 to 10 cm. long, 1 to 3 cm. broad, lyrate to pinnately divided or the lowermost occasionally undivided; the upper stem-leaves remote, sessile, and pinnately divided into small linear and entire to abruptly cuneate and unequally toothed lateral divisions; inflorescence a terminal few-headed corymbose cyme; heads 6 to 8 mm. high, radiate; involucre campanulate, glabrous, minutely calyculate; bracts of the involucre usually 21, linear-lanceolate, 3 to 5 mm. long, acute; ray-flowers 8 to 12; disk-flowers commonly 50 to 60; achenes hirtellous-puberulent.

Distribution: western Louisiana, Oklahoma, and Texas.

Specimens examined:

Louisiana: without locality, *Leavenworth* (Gray Herb. and Kew Herb.).

Oklahoma: Rock Creek, coll. of 1884, *Tufts* (U. S. Nat. Herb.); between Fort Cobb and Fort Arbuckle, coll. of 1868, *Palmer 462* (U. S. Nat. Herb.); near Indianola, *Pope* (Gray Herb.); Muskogee, May, 1894, *Schenck* (Field Mus. Herb.); near Paul's Valley, Garvin County, 19 April, 1913, *Stevens 108* (Mo. Bot. Gard. Herb.).

Texas: Dallas, 16 April, 1901, *Reverchon 558* (Mo. Bot. Gard. Herb.); in waste ground, Tarrant Co., 5 May, 1912, *Ruth 367* (Mo. Bot. Gard. Herb.); Waco, *Pace 122* (Mo. Bot. Gard. Herb.); Navarro Co., 22 May, 1880, *Joor* (Mo. Bot. Gard. Herb.); wet ground, Houston, May, 1872, *Hall 368* (U. S. Nat. Herb. and Field Mus. Herb.); Harrisburg, 24 April, 1899, *Eggert* (Mo. Bot. Gard. Herb.); Harris Co., 13 and 22 May, 1876, *Joor* (Mo. Bot. Gard. Herb.); vicinity of Huntsville, 6–12 May, 1910, *Dixon 516* (Field Mus. Herb.); Columbia, 6 April, 1899, *Bush 56* (Mo. Bot. Gard. Herb.); Columbia, 31 March, 1902, *Bush 1263* (Mo. Bot. Gard. Herb.); along Corpus Christi Bay, 21 March, 1894, *Heller 1476* (Gray Herb., U. S. Nat. Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Corpus Christi, 7 April, 1905, *Tracy 8927* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); low prairies near Rosenberg, 5 April, 1900, *Eggert* (Mo. Bot. Gard. Herb.); Richmond, 15 March, 1914, *Palmer 4954* (Mo. Bot. Gard. Herb.); Hungerford, 4 March, 1914, *Palmer 4844* (Mo. Bot. Gard. Herb.); Austin, March, 1870, *Bodin 52* (U. S. Nat. Herb.); "Bejar a la villa de Austin," *Berlandier 1741, 421* (Gray Herb.), CO-TYPE; near Belknap, 20 April, 1858, *Sutton Hays 515* (Field Mus. Herb.); Brazos, coll. of 1889, *Nealley 91, 280* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); Brazos, April, 1859, *Lindheimer* (Mo. Bot. Gard. Herb.); bottom land between Laredo and Palafox, *Schott* (Field Mus. Herb.).

21. **S. Millefolium** Torr. & Gray, Fl. N. Am. **2**: 444. 1843; Gray, Syn. Fl. N. Am. **1**^{2}: 392. 1884, and ed. 2, 1886; Chap-

man, Fl. Southern U. S., ed. 3, 266. 1897; Small, Fl. Southeastern U. S. 1305. 1903, and ed. 2, 1913.

An herbaceous perennial, glabrous or with a white floccose-tomentum at the base of the stem and in the axils of the leaves; stems 3 to 7 dm. high, striate; leaves bi–tri-pinnately dissected into linear segments; basal and lower stem-leaves petiolate, 1 to 2.5 dm. long, 1.5 to 6 cm. wide, the upper ones sessile; inflorescence terminating the stem in a corymbose cyme; heads 8 to 10 mm. high, radiate; involucre campanulate, sparingly calyculate, glabrous; bracts of the involucre 4 to 6 mm. long; ray-flowers 8 to 12; disk-flowers numerous, usually 50 to 60; achenes hirtellous-puberulent.

Distribution: mountains of North Carolina and South Carolina.

Specimens examined:

North Carolina: slope of Caesar's Head, 3 Sept., 1876, *Engelmann* (Mo. Bot. Gard. Herb.); without locality, coll. of 1888, *Boynton* (U. S. Nat. Herb.); dry, rocky places on White Oak Mountains, Polk Co., alt. 850 m., 4 May, 1897, *Biltmore Herb. 1301*[b] (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Skyuka Mountains, Polk Co., 25 May, 1899, *Churchill* (Gray Herb.).

South Carolina: Table Rock, coll. of 1842, *Buckley* (Gray Herb. and Mo. Bot. Gard. Herb.); "Carolina," *Fraser* (Gray Herb.), part of TYPE; Caesar's Head, Aug., 1876, *Canby* (U. S. Nat. Herb.).

22. S. tampicanus DC. Prodr. **6**: 427. 1837; Hemsl. Biol. Cent.-Am. Bot. **2**: 248. 1881, excl. plant of Wright.

S. Ervendbergii Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902; Field Col. Mus. Bot. Ser. **2**: 275. 1907.

Glabrous throughout; stem 4 dm. or more high, terete, striate, leafy; leaves thin, pinnately divided into cuneate to obovate, unequally dentate divisions; lower leaves petiolate, 1 to 3 dm. long, the upper ones sessile and amplexicaul by a large stipular-like base; inflorescence a terminal compound corymbose many-headed cyme; heads small, 5 to 7 mm. high,

radiate; involucre campanulate, glabrous, minutely calyculate; bracts of the involucre 21, linear-lanceolate, 3 to 4 mm. long; ray-flowers about 13; disk-flowers numerous, 70 to 90; achenes hirtellous along the ribs.

Distribution: eastern Mexico.

Specimens examined:

Tamaulipas: Tampico, coll. of 1827, *Berlandier 186* (Berlin Herb., tracing and fragments in Gray Herb.), CO-TYPE.

Vera Cruz: Wartemberg, near Tantoyuca, coll. of 1858, *Ervendberg 90* (Gray Herb.); without locality, *Liebmann 172* (Copenhagen Herb., tracing and fragments in Gray Herb.).

Puebla: near Metaltoyuca, alt. 240 m., 27 Feb., 1898, *Goldman 74* (U. S. Nat. Herb. and Gray Herb.).

San Luis Potosi: without definite locality, *Parry & Palmer 533* (Gray Herb.).

23. S. hypotrichus Greenm.[1]

S. Sanguisorbae Hemsl. Biol. Cent.-Am. Bot. **2**: 246. 1881, in part, not DC.

An herbaceous perennial; stem 7 dm. high, erect, striate, glabrous, somewhat purplish, branched above; leaves pinnately divided into cuneate to rhomboic-ovate dentate unequal divisions, glabrous above, crisp-hirsute beneath; lower leaves including the petiole 2 to 3 dm. long, 4 to 9 cm. broad, the upper stem-leaves sessile, semiamplexicaul and gradually reduced towards the terminal corymbose cyme; heads 8 to 10 mm. high, radiate; involucre campanulate, sparingly calyculate; bracts of the involucre usually 21, linear-lanceolate,

[1] **Senecio hypotrichus** Greenm. sp. nov. herbaceus perennis; caule erecto circiter 7 dm. alto tereti striato stramineo vel plus minusve purpurascenti glabro, superne ramoso; foliis pinnatifidis, inferioribus petiolatis usque ad 3 dm. longis, 4 to 9 cm. latis, superioribus sessilibus et semiamplexicaulibus gradatim reductis, laciniis anguste cuneatis vel obovatis vel rhombo-ovatis subcrenato-dentatis supra glabris subtus crispo-hirsutis; inflorescentiis terminalibus corymboso-cymosis; capitulis 8–10 mm. altis radiatis; involucri squamis plerumque 21 lineari-lanceolatis 5–6 mm. longis glabris; floseulis liguliferis saepius 13, ligulis oblongis, 6–7 mm. longis, 2.5 mm. latis, 4–5-nerviis; floribus disci 60–70; achaeniis glabris. —Region of San Luis Potosi, Mexico, alt. 1830–2440 m., coll. of 1878, *Parry & Palmer 533* (U. S. Nat. Herb.), TYPE. The Gray Herbarium specimen of Parry and Palmer's No. 533 differs from the United States National Herbarium specimen above cited in having glabrous leaves, smaller and more numerously flowered heads and hirtellous achenes; it has been referred to *S. tampicanus* DC.

5 to 6 mm. long, glabrous; ray-flowers 13, rays oblong, 6 to 7 mm. long, 2.5 mm. broad, 4–5-nerved; disk-flowers 60 to 70; achenes glabrous.

Distribution: central Mexico.

San Luis Potosi: "region of San Luis Potosi," alt. 1830–2440 m., coll. of 1878, *Parry & Palmer 533* (U. S. Nat. Herb.), TYPE.

24. S. Sanguisorbae DC. Prodr. **6**: 427. 1837; Hemsl. Biol. Cent.-Am. Bot. **2**: 246, 1881, in part; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

An herbaceous perennial; stem erect, 3 to 10 dm. high, striate, glabrous, simple or branched; leaves pinnately divided, the radical and lower stem-leaves petiolate including the petiole 1 to 4 dm. long, 3 to 13 cm. broad, glabrous on both surfaces or slightly subarachnoid beneath, the upper stem-leaves sessile and more or less amplexicaul; lateral leaf-segments oblong-cuneate to oblong-ovate, 1 to 7 cm. long, .3 to 5.5 cm. broad, rather coarsely dentate, the terminal segment usually broadly obovate; inflorescence a terminal many-headed corymbose cyme; heads 6 to 8 mm. high, radiate; involucre narrowly campanulate, sparingly calyculate; bracts of the involucre 8 to 13, linear-lanceolate 4.5 to 6 mm. long, glabrous; ray-flowers 5 to 8; disk-flowers 15 to 25; achenes glabrous.

Distribution: southern Mexico.

Specimens examined:

Hidalgo: by brooks, Sierra de Pachuca, alt. 3050 m., Aug., 1902, *Pringle 9959* (Gray Herb. and Mo. Bot. Gard. Herb.); Sierra de Pachuca, 1 Sept., 1903, *Rose & Painter 6739* (Gray Herb.).

Mexico: Toluca, coll. of 1854, *Schaffner* (Gray Herb. and Berlin Herb.); Valley of Mexico, Sante Fe, *Bourgeau 832* (Gray Herb., U. S. Nat. Herb., Berlin Herb., and Kew Herb.); without locality, *Gregg 691* (Mo. Bot. Gard. Herb.); Cima, 24 Aug., 1910, *Orcutt 3767* (Mo. Bot. Gard. Herb.); in moist soil along brooks, Mt. Ixtaccihuatl, alt. 3050–3350 m., Nov., 1905, *Purpus 1514* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); in moist soil, Mt. Popocatepetl, Sept., 1908, *Purpus*

3044 (Field Mus. Herb. and Mo. Bot. Gard. Herb.); Mt. Popocatepetl, 7 and 8 Aug., 1901, *Rose & Hay 6069* (U. S. Nat. Herb.); without locality, *Uhde 582, 602, 603, 609, 624* (Berlin Herb.); without locality, coll. of 1848–49, *Gregg 673* (Gray Herb.).

Michoacan: Angangueo, *Hartweg 313* (Berlin Herb.); cool summits of mountains near Patzcuaro, 2 Aug., 1892, *Pringle 4129* (Gray Herb., U. S. Nat. Herb. and Mo. Bot. Gard. Herb.).

25. S. pinnatisectus DC. Prodr. **6**: 427. 1837; Hemsl. Biol. Cent.-Am. Bot. **2**: 245. 1881; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

Cineraria pinnata La Llav. & Lex. Nov. Veg. Descr. fasc. 1, 26. 1824.

An herbaceous perennial; stem erect, 4 dm. or more high, striate, glabrous or slightly tomentulose; leaves pinnately divided, the lower petiolate, including the petiole 1 to 3 dm. long, 3 to 8 cm. broad, the upper sessile and amplexicaul, at first white floccose-tomentulose, later glabrate except for the persistent tomentum along both sides of the rhachis; lateral divisions of the leaf narrowly oblong, sharply serrate-dentate, terminal division obovate-cuneate; inflorescence a terminal compound compact corymbose cyme; heads numerous, 6 to 7 mm. high, radiate; involucre calyculate, glabrous; bracts of the involucre usually 13; ray-flowers commonly 6 to 8; disk-flowers 15 to 20; achenes glabrous.

Distribution: southern Mexico.

Specimens examined:

Hildalgo: Real del Monte, *Ehrenberg 386* (Berlin Herb. and Gray Herb.), also *386*[a], *386*[b] (Berlin Herb.); Real del Monte, coll. of 1830, *Graham* (Gray Herb. and Kew Herb.).

Michoacan (?): Angangueo, *Chrismar* (Berlin Herb.); "Cuesta de las papao Angangueo," *Schiede* (Berlin Herb.).

Mexico, without definite locality: *Bates, Mackenzie,* and also *Parkinson* (Kew Herb.).

This species is closely related to the preceding, but differs in the narrower lateral leaf-segments, slightly smaller heads,

and persistent floccose tomentum along the rhachis or midrib.

26. S. coahuilensis Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902; Field Col. Mus. Bot. Ser. **2** : 275. 1907. Plate 19, fig. 2.

An herbaceous perennial, glabrous or essentially so throughout; stem erect, 3 to 8 dm. high, branched, striate; leaves pinnately divided into obovate to subreniform cuneate-dentate divisions, thickish and firm in texture, glabrous on both surfaces or slightly pubescent on the veins beneath; lower leaves including the petiole 1 to 3 dm. long, 2 to 5 cm. broad, the upper stem-leaves sessile and amplexicaul; inflorescence terminating the stem and branches in a compound corymbose cyme; heads 7 to 10 mm. high, radiate; involucre campanulate, calyculate with a few small bracteoles, glabrous; bracts of the involucre 13 to 18, linear-lanceolate, 4 to 6 mm. long, thickish; ray-flowers 8 to 10, rays oblong, 3 to 5 mm. long, 4-nerved; disk-flowers 35 to 45; achenes ribbed, glabrous.

Distribution: northern Mexico.

Coahuila: Lerios, Feb. to Oct., 1880, *Palmer 755* (Gray Herb., Kew Herb., and U. S. Nat. Herb.), TYPE; without locality, coll. of 1848-49, *Gregg 403* (Gray Herb. and Mo. Bot. Gard. Herb.).

27. S. leonensis Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902; Field Col. Mus. Bot. Ser. **2** : 276. 1907. Plate 19, fig. 1.

An herbaceous perennial, more or less lanate-tomentose throughout, somewhat glabrate in age; stem 2 to 3 dm. high, leafy at the base, essentially naked above; leaves petiolate, pinnately divided, including the petiole 8 to 12 cm. long, about 3 cm. broad, at first lanate-tomentulose on both surfaces, later glabrate; divisions of the leaf rather coarsely, somewhat unequally and sharply dentate, the terminal segment subreniform, the lateral ones (3 to 6 on either side) obovate-cuneate; heads few, about 1 cm. high, radiate; involucre campanulate, slightly calyculate and, as well as the bracteate peduncle, tomentulose; bracts of the involucre about 13; disk-flowers numerous, 50 to 60; achenes pubescent.

Distribution: northern Mexico.

Specimen examined:

Nuevo Leon: Sierra Madre, near Monterey, 1 June, 1889, *Pringle 2894* (Gray Herb.), TYPE.

28. **S. montereyana** Wats. Proc. Am. Acad. **25** : 155. 1890; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902.

An herbaceous perennial, more or less white-tomentose throughout; stems one to several, 2.5 to 4 dm. high, from a rather stout ascending rootstock; leaves mostly radical, including the petiole 1 to 2 dm. long, 1.5 to 3 cm. broad, pinnately divided into narrow, oblong, cuneate to sublinear, entire or few-toothed divisions, at first white-floccose-tomentose on both surfaces, somewhat glabrate above; heads few, 10 to 12 mm. high, radiate, on long naked peduncles; involucre campanulate, calyculate with minute bracteoles, tomentose; bracts of the involucre slightly shorter than the numerous flowers of the disk; ray-flowers about 12; achenes hirtellous-pubescent.

Distribution: northern Mexico.

Specimens examined:

Nuevo Leon: dry shaded ledges of the Sierra Madre, near Monterey, 27 June, 1888, *Pringle 1922* (Gray Herb., U. S. Nat. Herb., Kew Herb., and Mo. Bot. Gard. Herb.), TYPE.

29. **S. zimapanicus** Hemsl. Biol. Cent.-Am. Bot. **2**: 248. 1881; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** :19. 1902.

An herbaceous perennial; stems 3 to 4.5 dm. high, simple, leafy below, nearly naked above, striate, more or less pubescent with flaccid-hirsute, jointed, and somewhat matted hairs; leaves mostly basal, sessile or essentially so, 3 to 18 cm. long, 1 to 3 cm. broad, pinnately lobed or divided into oblong-ovate dentate divisions, flaccid-hirsute or subarachnoid-pubescent on both surfaces, more densely so beneath; inflorescence a terminal corymbose few-headed cyme; heads large, 10 to 14 mm. high, conspicuously calyculate, radiate; bracts of the involucre commonly 21 (15–21) linear-lanceolate, 7 to 9 mm. long, thickish, glabrous except at the penicillate tip; ray-

flowers 12 to 15, rays oblong, 10 to 12 mm. long; disk-flowers numerous; achenes about 3 mm. long, ribbed, slightly pubescent on the ribs.

Distribution: eastern Mexico.

Specimens examined:

Hildago: Zimapan, *Coulter 423* (Kew Herb.), TYPE.

Tamaulipas: near Miquihuana, alt. 2140 to 2740 m., 10 June, 1898, *Nelson 4492* (Gray Herb. and U. S. Nat. Herb.).

SECT. 5. BOLANDERIANI Greenm.

§ 5. BOLANDERIANI Greenm. Monogr. Senecio, I. Teil, 22, 23. 1901, and in Engl. Bot. Jahrb. 32 : 18, 19. 1902.

Slender, herbaceous perennials; stems erect or nearly so, 1 to 5 dm. high, from a slender more or less horizontal rootstock; leaves undivided and orbicular-ovate to pinnatifid; heads of medium size, about 1 cm. high, radiate; achenes glabrous. Sp. 30–32.

A. Stems 1.5 to 5 dm. high, leafy to the inflorescence.
  a. Leaves usually pubescent beneath; bracts of the involucre 6 to 9 mm. long, more or less hairy.. *30. S. Bolanderi*
  b. Leaves glabrous on both surfaces; bracts of the involucre 5 to 6.5 mm. long, glabrous ..... *31. S. Harfordii*
B. Stems 1 to 2 dm. high, leafy only at the base..... *32. S. Flettii*

30. S. Bolanderi Gray, Proc. Am. Acad. **7** : 362. 1868; Bot. Calif. **1** : 411. 1876, in part; Syn. Fl. N. Am. **1**^{2} : 392. 1884, and ed. 2, 1886, in part; Howell, Fl. N. W. Am. **1** : 379. 1900, in part; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902.

A slender herbaceous perennial; stems ascending or erect, from a creeping rootstock, 1.5 to 5 dm. high, striate, often somewhat purplish; radical and lower stem-leaves undivided and crenately lobed-dentate to pinnately divided into oblong, obovate to subrotund, crenate to sharply dentate divisions, glabrous above, usually pubescent beneath, including the petiole .5 to 1.5 dm. long, 1 to 3 cm. broad; the upper stem-leaves sessile; inflorescence terminating the stem in a few-headed subcorymbose cyme; heads 10 to 12 mm. high, radiate; involucre campanulate, calyculate, usually tawny pubescent; bracts of the involucre about 13, linear-lanceolate, 6 to 9 mm.

long; ray-flowers 5 to 8; disk-flowers rather numerous, 25 to 45; achenes glabrous.

Distribution: California and Oregon, near the coast.

Specimens examined:

California: on sand-stone bluffs at the mouth of the river below Mendocino City, May, 1866, *Bolander 4816* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.), TYPE; Humboldt, coll. of 1868–69, *Kellogg & Harford 539* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb); Humboldt, coll. of 1866, *Kellogg 539* (Gray Herb.); Redwoods, Eel River, coll. of 1878, *Rattan 33* (Gray Herb.); near Crescent City, Del Monte Co., June, 1892, *Burt-Davy & Blasdale 1072* (Field Mus. Herb.).

Oregon: Coast Mountains, Lat. 42°, June, 1884, *Howell 162* (Gray Herb.); Newport, June, 1892, *Mulford* (Mo. Bot. Gard. Herb.).

31. **S. Harfordii** Greenm. Contr. U. S. Nat. Herb. **11**: 597. 1906.

S. Bolanderi var. *oregonensis* Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

A slender herbaceous perennial, glabrous throughout; stem erect or ascending from a creeping rootstock, 2 to 5 dm. high, usually leafy; leaves mostly pinnately divided into cuneate to subrotund crenate to laciniate-dentate divisions; the radical and lower stem-leaves petiolate, including the petiole 4 to 14 cm. long, 1 to 5 cm. broad, occasionally undivided, subrotund and crenately lobed and the lobes again crenate-dentate, thin in texture, pale green in the dried state; the upper stem-leaves sessile; inflorescence a few-headed corymbose cyme; heads 8 to 10 mm. high, radiate, including the conspicuous yellow rays 1.5 to 2 cm. in diameter; bracts of the involucre usually 13, narrowly lanceolate, 5 to 6 cm. long, acuminate, acute, glabrous; ray-flowers usually 5 (–8); disk-flowers 15 to 25; mature achenes 2.5 to 3.5 mm. long, glabrous.

Distribution: mountains of Washington and Oregon.

Specimens examined:

Washington: on mountains near the Lower Cascades, Skamania Co., 29 May, 1886, *Suksdorf* (Gray Herb.); in

woods, Lower Cascades, 29 May, 1887, *Suksdorf 872* (Mo. Bot. Gard. Herb.); summit of Mt. Adams, 4 Aug., 1899, *Flett 1087* (Piper Herb.).

Oregon: Rooster Rock, June, 1877, *Howell* (Gray Herb.); Cascade Mountains, 31 May, 1868–69, *"Kellogg & Harford,"* namely *Harford & Dunn 540* (Gray Herb.), TYPE; near Bonneville, Multnomah Co., 11 July, 1885, *Suksdorf 572* (Gray Herb.); Multnomah Falls, 25 June, 1904, *Piper 6212* (Gray Herb.); Bonneville, 24 June, 1905, *Palmer* (U. S. Nat. Herb.).

32. S. Flettii Wiegand, Bull. Torr. Bot. Club **26**: 137, *pl. 355.* 1899; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902; Piper, Contr. U. S. Nat. Herb. **11**: 597. 1906.

An herbaceous perennial, 1 to 2 dm. high, glabrous throughout; leaves mostly basal, petiolate, including the petiole 4 to 12 cm. long, 1.5 to 2 cm. broad, undivided, ovate-orbicular and crenate-dentate to pinnately parted, upper stem-leaves few, 1 to 3, incisely pinnate to linear and bractiform; inflorescence terminating the stem in a few-headed corymbose cyme; heads about 1 cm. high, radiate; involucre narrowly campanulate, sparingly calyculate; bracts of the involucre 8 to 13, linear-lanceolate, 5 to 6 mm. long, thickish, glabrous; ray-flowers commonly 5; disk-flowers about 20; achenes glabrous.

Distribution: Washington.

Specimens examined:

Washington: loose rocks, Olympic Mountains, alt. 1830 m., 27 Aug., 1898, *Flett 801* (Piper Herb.), CO-TYPE; Olympic Mountains, Clallam Co., Aug., 1900, *Elmer 2620* (Mo. Bot. Gard. Herb.); Angeles, Clallam Co., 29 June, 1908, *Flett 3351* (U. S. Nat. Herb.); in volcanic sands, Olympic Mountains, alt. 1525 m., Sept., 1890, *Piper 929* (Gray Herb., Mo. Bot. Gard. Herb., and U. S. Nat. Herb.); crevices of volcanic rock, Olympic Mountains, alt. 2135 m., Aug., 1895, *Piper 2196* (U. S. Nat. Herb., Gray Herb., and Piper Herb.); Yakima Region, coll. of 1882, *Brandegee 176* (Mo. Bot. Gard. Herb.).

(To be continued.)

Explanation of Plate

PLATE 17

Senecio mohavensis Gray
California

From the type specimen, Lemmon No. 3129, in the Gray Herbarium of Harvard University.

GREENMAN—MONOGRAPH OF SENECIO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 18

Senecio durangensis Greenm.
Mexico

From the type specimen, Pringle No. 10105, in the Gray Herbarium of Harvard University.

GREENMAN—MONOGRAPH OF SENECIO

Explanation of Plate

PLATE 19

Fig. 1. *Senecio leonensis* Greenm.
Mexico

From the type specimen, Pringle No. 2894, in the Gray Herbarium of Harvard University.

Fig. 2. *Senecio coahuilensis* Greenm.
Mexico

From the type specimen, Palmer No. 755, in the Gray Herbarium of Harvard University.

GREENMAN—MONOGRAPH OF SENECIO

Explanation of Plate

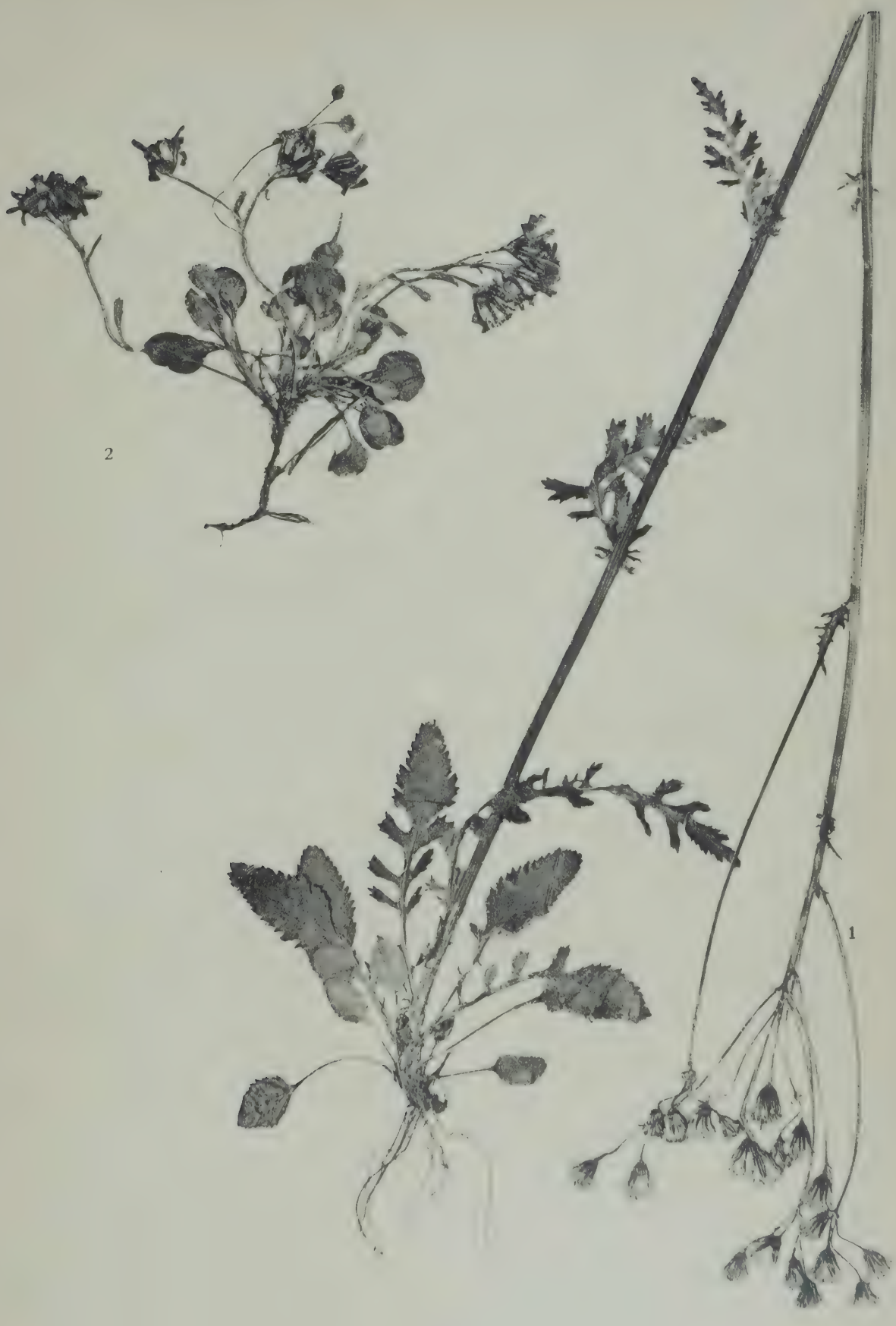
PLATE 20

Fig. 1. *Senecio Burkei* Greenm.
Canada

From Macoun's No. 69359 in the Gray Herbarium of Harvard University.

Fig. 2. *Senecio saxosus* Klatt
United States

From Baker's No. 770 in the Herbarium of the Missouri Botanical Garden.



GREENMAN—MONOGRAPH OF SENECIO

THE THELEPHORACEAE OF NORTH AMERICA. IV[1]

Exobasidium

EDWARD ANGUS BURT

Mycologist and Librarian to the Missouri Botanical Garden
Associate Professor in the Henry Shaw School of Botany of Washington University

EXOBASIDIUM

Exobasidium Woronin, Naturforsch. Ges. Freiburg Verhandl. **4**: 397–416. *pl. 1–3.* 1867.—Saccardo, Syll. Fung. **6**: 664. 1888.—Hennings, in Engl. & Prantl, Nat. Pflanzenfam. (**I**.1**) : 103. 1897.

The type species of the genus is *Exobasidium Vaccinii* Fuck. ex Wor.

Fungi parasitic in leaves, shoots, and flowers, which they deform more or less, producing on the surface of these organs an effused hymenium, rarely composed of basidia alone and more usually felt-like and composed chiefly of interwoven hyphae bearing basidia and conidiophores; basidia simple; spores white, simple or septate.

Exobasidium resembles so closely in the thinness of its fructifications such species of *Corticium* and *Peniophora* as *Corticium byssinum, Peniophora asperipilata, P. pilosa,* and *P. subalutacea* that I follow Saccardo and include it with the above genera in the *Thelephoraceae.* Hennings in Engler & Prantl's 'Die Natürlichen Pflanzenfamilien,' has raised *Exobasidium* to ordinal rank but this is not justified by the structure of the many fructifications of *Exobasidium* which I have sectioned; the illustrations in text-books of the structure in section of the fructification are decidedly diagrammatic and simplified.

In his work already cited, Woronin gives a detailed account of the morphology and life history of *Exobasidium Vaccinii* and illustrates this account with three double plates. The interest in this fungus which Woronin's work aroused has

[1] Issued October 8, 1915.

Note.—Explanation in regard to the citation of specimens studied is given in Part I, Ann. Mo. Bot. Gard. 1: 202, footnote.

resulted in the publication of other species by various authors, whose descriptions contrast sharply with that of Woronin in giving little weight to the morphological characters of the fungus under consideration, but extended description of the form and color of the gall of a particular collection, with passing reference to the occurrence of the fungus upon a hitherto unpublished host. In case of the galls, the descriptions usually fail to state what other forms besides the one mentioned the galls may have on other organs of the new host and likewise omit mention of the different forms they may have at other times in the year than the particular time at which the type collection was made. Woronin's description of *E. Vaccinii* was based upon field observations extended through two seasons, during which more than a thousand specimens were collected. He gives one double page colored plate to show the various types of galls produced by the different organs of *Vaccinium vitis-idaea.*

Plate 21 is a photographic reproduction, reduced one-fifth, of Woronin's colored plate; it shows the forms of galls as determined by the particular organ of the host, *Vaccinium vitis-idaea,* which makes hypertrophic response to local stimulation by the parasitic fungus. A local change of color from green to some shade of red is common in plant portions infested with *Exobasidium.* In the photographic reproduction of Woronin's plate the reddened areas of the original appear light colored. In fig. 1, the left side of the uppermost leaf was attacked by the fungus, producing what I term a leaf spot gall. The affected region of the leaf is reddened on the upper side and bears the fructification which may be felty or scurfy on the under side; this leaf is not distorted much in form and thickness.

Figures 2–9 present leaf galls, reddened on the upper side of the leaf and distorted and thickened by hypertrophic growth so as to become more or less concave with respect to the upper surface. I designate this form of gall as leaf concavity.

Figures 10–17 illustrate shoot galls, in the production of which, stems of the current season's growth have been greatly

enlarged and have turned pale and slightly pink under the stimulus of the infecting fungus. In figs. 10–15 the lateral axillary buds along the infected stem have abnormally enlarged by the stimulation of the fungus and have developed in several instances short, delicate, wax-like or coralloid branchlets of carmine color. Such branchlet shoot galls are beautiful objects in their vegetative condition; they constitute a noteworthy type of gall which is quite different in appearance from the more common leaf galls, produced in response to local infection of leaves. Nevertheless, the common cause of these different gall forms is well brought out by Woronin's illustrations, especially by figs. 11, 12, 13, and 15. Upon shoot galls similar to the above, there have been published *Exobasidium Andromedae* Karst. non Peck for the shoot galls of *Andromeda polifolia, E. cassiopes Peck* for the shoot gall of *Cassiope Mertensiana,* and *E. Oxycocci* Rostrup for that of *Oxycoccus palustris.*

Figures 16–18 show the flower type of gall of *Vaccinium vitis-idaea,* that is, the abnormal growth form made by individual flowers in response to the stimulation of their tissues by the fungus. That both the flower gall and the leaf gall have a common cause has been brought out well by the selection of the specimens used for figs. 16 and 17. In fig. 18 there is presented local infection of a single flower. This is important because isolated flower galls upon a new host have in some cases been regarded as *prima facie* evidence that they have been caused by a new species of *Exobasidium.*

Other host plants produce some types of galls, when infected with *Exobasidium,* which were not figured by Woronin for *Vaccinium vitis-idaea* but which are more or less common. Such gall types are:

(a) Leaf type in which scattered whole leaves of the host are infected. These leaves redden more or less on the upper side and bear on the whole under side the scurfy or felty fructification but are not notably thickened or deformed. This gall differs from the leaf spot gall of Woronin's fig. 1 merely in having the whole of the leaf infected.

(b) Shoot gall with all the leaves toward the tip of the

shoot infected but not deformed. These leaves may be almost normally green on the upper side or they may be more or less reddened, sometimes to carmine red; on the under side they become clothed with the felty fructification of the fungus but the leaves are not deformed. This is merely a more general infection than the leaf type *a,* described above, and is often associated with it on the same plant as well as with the leaf spot and leaf concavity forms.

(c) Bag gall of *Andromeda ligustrina.* This is the extreme in gall production. This gall finally becomes a hollow bag which attains a maximum size of 10–15 cm. in length by 5–10 cm. in diameter. These bag galls are either terminal or lateral on leafy shoots of the current season's growth. When lateral, such a gall has the morphological position of a leaf.

(d) Bud gall of *Symplocos tinctoria.* The expanding leaf buds are deformed into a subglobose mass which may be 3–3½ cm. in diameter. In this gall, the undeveloped stem of the bud is greatly enlarged and the individual leaves of the bud are greatly thickened and deformed.

In North America, we have a large number of species of *Ericaceae* which produce galls when infected by *Exobasidium.* The specimens which have accumulated under *Exobasidium* in herbaria show that none of the gall forms which I have designated under distinctive names in the preceding paragraph are isolated forms. Favorable hosts show a connection and gradation between the various gall forms as intimate as that presented by Woronin for *Vaccinium vitis-idaea.* However, the terms which I employ are useful for contrasting and comparing the data presented by the specimens which I have studied. These data are later given in tabular form.

The microscopic examination of an Exobasidium gall shows that it is composed principally of the tissues of the host plant. Hyphae of the fungus ramify about between the cells of the host and, in the galls in which deformation has taken place, the presence of the fungous hyphae has caused the host both to multiply and enlarge its cells in the infected region. The gall is, therefore, a direct product of the host plant, which

is stimulated to growth by the presence of the parasitic vegetative hyphae, by absorption of organic products from the host, and, undoubtedly, by excreta from the hyphae. We may see from Woronin's figures that the various organs of a given host produce different galls when infected by the same fungus; from which we may conclude that the several organs of the host make different growth responses to the same stimulating cause. We have in the host itself, in its several organs, and also in the age of tissues of these organs, as I shall point out later, factors not only able to produce, but actually producing, diversity in gall form even though but a single species of *Exobasidium* is the parasitic stimulant. Of what value, then, is the form of the gall as a taxonomic character for species of *Exobasidium?*

The different organs of the host differ in the resistance which they offer to infection by *Exobasidium.* Woronin notes in his work cited that out of more than a thousand specimens of *Exobasidium Vaccinii,* only twelve showed flower galls. Hence the flowers of *Vaccinium vitis-idaea* are much less subject to infection than the leaves. In only the one case, which he illustrates by fig. 18, did he observe local infection of a flower. In figs. 16 and 17, the infected flowers are borne on infected shoots and may have become infected through these shoots. We may therefore conclude that in a given host a high resistance of certain organs to infection by *Exobasidium* restricts the galls for that host to fewer organs and to a smaller number of forms than in some other host with a lesser resistance.

That the age of the organs, or their cells, of a host is an important factor in the determination of gall form is apparent if one observes throughout a season the succession of galls produced by a favorable host. In this connection Richards[1] has stated, "and also on Gaylussacia resinosa in the earliest formed distortions, whole shoots are transformed. Later in the season the Exobasidium forms only slight local distortions on the leaves, and still later one finds forms which do not distort the tissues of the host plant at all, but simply form a

[1]Bot. Gaz. 21 : 107. 1896.

scurf on the lower side of the leaves. The same succession is found in the forms on Andromeda down to the last mentioned." Richards determined by culture experiments that the remarkable bag galls of *Andromeda ligustrina* are merely early (June in Massachusetts) productions under the same specific fungous stimulus which later in the season induces leaf concavities on this host. The account of his experiments[1] may be summarized as follows: During July, Exobasidium spores were removed with suitable precautions from fresh mature bag galls of *Andromeda ligustrina* and were immediately transferred to buds and young leaves of experimental plants of the same species, which were isolated in a moist chamber. In about ten days faint discolorations of the leaves were noticed, at first yellowish and then pink. About five days later, the spots which had considerably enlarged, began to show unmistakable signs of thickening, forming the peculiar concavities in the leaves seen in other Exobasidia. In external form, and also in the matter of basidia and spores, this distortion resembled precisely the leaf form on *Andromeda ligustrina,* and indicates that the *Exobasidium* which produces the bag galls of the young buds is identical with the fungus which produces the leaf form found later in the season.

The foregoing presentation of the Exobasidium gall as a growth response of the host under stimulation by the fungus shows that very different forms of galls and differences in regard to abundance of each form on a host may result—

(a) From the different organs making the response.

(b) From differences in resistance of the several organs, which, in many cases, may undoubtedly be so great as to give complete immunity for certain organs.

(c) From the age of the organ attacked.

Since the host produces a great variety of gall forms as growth responses to attack by a single species of *Exobasidium*, how are we to decide whether a given gall form is ever sufficiently distinct to entitle its causative organism to separate specific rank? Gall forms are host products to so large an

[1] *loc. cit.*, p. 105.

extent that they can have little, if any, value for discriminating between species of *Exobasidium*. Into the formation of such galls so many other factors besides the Exobasidium hyphae enter that it is impossible to consider galls as homologous with the fructification of an ascomycete or that of a toadstool, and they should not be used therefore in the way these true fungous fructifications are used for affording in their form specific characters. As a matter of fact, the layer of basidia and conidia-bearing hyphae at the outside of the gall comprise the whole fructification of the parasitic fungus; this layer alone is morphologous with a toadstool. The mere form of the foreign substratum covered by the resupinate fructification of *Exobasidium* should have no greater taxonomic weight than it has in the closely related genus *Corticium*.

We should now consider the distribution of *Exobasidium Vaccinii* as a parasite upon various genera and species of the *Ericaceae*. Woronin limited his investigation of *E. Vaccinii* to what he observed on *Vaccinium vitis-idaea* and left the matter there for other investigators to go on with, if they were so disposed. As the collections which are made on this host nearly always show the fungus occurring in leaf spot galls and leaf concavity galls, and since these forms of galls are the only ones on this host common enough for distribution in published exsiccati, the species *Exobasidium Vaccinii* seems to have become altogether too closely associated with, and limited in mycological practice to, merely the very commonest gall forms which are produced under stimulation by *E. Vaccinii*. For example, Shear[1] states, "The typical form of *Exobasidium Vaccinii* occurs on *Vaccinium vitis-idaea*, producing hypertrophied spots on the leaves. No record has been found of the occurrence of hypertrophied shoots on this host similar to those found on cranberry plants. Rostrup[51] seems to have been the first to describe this form. In 1883 he reported it as occurring on *Oxycoccus palustris* in Denmark."

[1] Cranberry Diseases. U. S. Dept. Agr., Bur. Pl. Ind., Bul. 110: 36. 1907.

Without doubt, this misapprehension of the galls produced by *Vaccinium vitis-idaea* is due to the scarcity of copies of Woronin's original account of *Exobasidium Vaccinii,* for Woronin is at great pains to show that to *E. Vaccinii* are due both shoot galls and flower galls.

That the erroneous tendency of limiting to *E. Vaccinii* the production of only the commonest leaf galls is potent, is apparent from inspection of the table towards the close of this paper where under the heading, "Exobasidium Vaccinii (Fuck.) Wor. The following have been referred here invariably" there are grouped all Exobasidium galls produced by *Vaccinium vitis-idaea, V. vacillans, V. arboreum, V. pennsylvanicum, V. stamineum, Gaylussacia frondosa, G. resinosa, Arctostaphylos uva-ursi, A. nevadensis, Arbutus Menziesii, Rhododendron canadense, R. maximum,* and *Lyonia jamaicensis.*

Our *Gaylussacia frondosa* and *G. resinosa* of this list merit some detailed consideration for they compare very favorably with *Vaccinium vitis-idaea* as hosts for *Exobasidium Vaccinii.* The galls of these two species of *Gaylussacia* include during the season two shoot forms, leaf concavity type, leaf spot type, and the flower type. The flower type of gall is probably very rare; I have seen a dried herbarium specimen of it collected by Dr. Farlow, at Brewster, Massachusetts, and two others, preserved in alcohol in Seymour Herbarium, one of which was collected by A. B. Seymour, at Woods Hole, Massachusetts, and the other by Mrs. Pier, at Biddeford, Maine. These flower galls have a diameter of 10–12 mm.; all the floral organs are enlarged as in case of the flower galls illustrated by Woronin. Bartholomew collected and distributed in his 'Fungi Columbiani,' 3429, the shoot gall of the wax-like or coralloid type such as is produced by *Vaccinium vitis-idaea. Gaylussacia resinosa* very frequently produces as its earliest galls the other form of shoot gall with all the leaves felty on the whole under surface, more or less reddened above, and not deformed. Such a shoot gall is produced by *Vaccinium Myrtillus* in Europe; it has usually been regarded by European mycologists as due to *Exobasidium Vaccinii.* Its regular

occurrence in North America in a series of *E. Vaccinii* forms confirms the correctness of the reference.

As we take up the consideration of North American species of *Exobasidium* which have been published since 1867, we find that in nearly all cases peculiarities of galls have furnished the distinctive portion of the description. These odd or striking forms of galls have been discovered upon new hosts, as was to be expected, for a new host species would without doubt have composition and properties at least slightly different from those of *Vaccinium vitis-idaea*—so different that the growth response, i. e., the gall of this new host, might differ somewhat, perhaps differ notably, from that of *V. vitis-idaea*, even though the stimulus should be given by the same fungus. Two of the specific names to be considered are based entirely upon the occurrence of *Exobasidium* on a new host, and the other eight are founded upon more or less noteworthy galls. Reference to the second division of my table shows that gall form rather than host has caused the publication of specific names in *Exobasidium*.

Exobasidium Peckii, for example, was published as the cause of flower galls produced by *Andromeda Mariana*. Its flower galls are produced so frequently that they attracted attention; leaf concavity galls are common here also. The morphological characters of the fungous cause of these galls agree closely with those of *Exobasidium Vaccinii*, and the galls themselves are of types that *Vaccinium vitis-idaea* produces under stimulation by *Exobasidium Vaccinii*. No evidence of any nature has been offered tending to show that *E. Peckii* is not *E. Vaccinii* in all respects. The frequent production of flower galls by *Andromeda Mariana* can be simply accounted for as due to the susceptibility of the young flower to infection by the fungus, that is, to a special property of this host. I regard *Exobasidium Peckii* as a synonym of *E. Vaccinii*.

In connection with the discussion of *E. Peckii*, attention should be called to occasional flower galls produced by *Lyonia* (*Andromeda*) *ferruginea*. I have seen only four specimens of these galls, two from Georgia and two from Florida. All

resemble monstrous flowers—up to 5 cm. long in the dried state—with all floral organs enlarged proportionally, as in the flower galls of *Andromeda Mariana, Gaylussacia resinosa,* and *Vaccinium vitis-idaea.* Only flower galls are as yet known to me for *Lyonia ferruginea,* but as the morphological characters of the fungus found on the galls are those of *Exobasidium Vaccinii,* I regard these galls as similar to those of *Andromeda Mariana* but much larger and due to *Exobasidium Vaccinii.* The large size of these Lyonia galls is the expression of the growth response of the flower tissue of this host. It will be interesting if further collections of this host show that only the flowers are susceptible to infection by *Exobasidium.*

Exobasidium Oxycocci was proposed as a name for the fungus causing the shoot galls of wax-like or coralloid habit which are produced by *Oxycoccus palustris.* Similar galls are produced in the United States by *Vaccinium macrocarpon* and *V. intermedium.* Shoot galls of *V. macrocarpon* are illustrated in color by Shear[1] and also the leaf spot and leaf concavity galls which this host produces. The morphological characters of the fungus producing the shoot galls on the cranberry species of *Vaccinium* are the same as those of *Exobasidium Vaccinii;* the galls produced by cranberry plants are such as *E. Vaccinii* produces. As there is no evidence of any kind that *E. Vaccinii,* common throughout the same region, does not cause the cranberry galls, the name *E. Oxycocci* seems quite unnecessary.

Exobasidium Cassiopes and *E. Karstenii* have been published as causes of the shoot galls produced by *Cassiope Mertensiana* and *Andromeda polifolia* respectively. These shoot galls are of the wax-like or coralloid type such as *Vaccinium vitis-idaea* produces under stimulation by *Exobasidium Vaccinii.* As the morphological characters of the so-called *E. Cassiopes* and *E. Karstenii* are those of *E. Vaccinii,* and as no evidence has ever been presented that *E. Vaccinii* does not cause the galls referred to, *E. Cassiopes* and *E. Karstenii* should also be regarded as synonyms of *E. Vaccinii.*

[1] *loc. cit., pl. 8.*

Exobasidium Andromedae Peck is based on the bag gall produced by *Andromeda ligustrina.* This gall described in detail on a preceding page, is so very large and remarkable in structure that it did seem that here, if anywhere, must be the anomaly for higher fungi of a fungous cause, specifically different from *Exobasidium Vaccinii,* yet having the same morphological characters. From this point of view, Richards' experiment,[1] already described, of growing on the leaves of *Andromeda ligustrina* a July crop of leaf concavity galls from spores produced by a bag gall which had matured at the beginning of July, was very illuminating. It showed that such a bag gall is noteworthy only because it shows peculiar properties inherent early in the season in shoots and leaves of *Andromeda ligustrina,* that this bag gall belongs in the series with, and is caused by, the same fungus as the leaf concavity galls such as *Exobasidium Vaccinii* produces.

Richards made other experiments tending to show that *E. Vaccinii* produces the bag galls on *Andromeda ligustrina.* He demonstrated that the latter species is not immune to undoubted *Exobasidium Vaccinii,* that it is as susceptible to such spores as to those produced by its own bag galls. In July, spores of *E. Vaccinii* gathered from leaf concavity galls of *Gaylussacia resinosa* were transferred to buds and young leaves of *Andromeda ligustrina.* After about the same lapse of time as when spores from the bag galls were used, there appeared on the Andromeda leaves infected with *Exobasidium Vaccinii* distortions very similar to those produced by spores from the bag galls. As the large bag gall was the only occasion for the name *E. Andromedae* Peck, I agree with Richards that this name is a synomym of *E. Vaccinii.*

In confirmation from the herbarium side of the correctness of the above conclusion, I have a specimen collected in Idaho by Professor Piper, 772, on *Menziesia glabella,* which has a small terminal bag gall such as is produced by *Andromeda ligustrina,* and also a leaf concavity gall.

In the light of what we now know about bag galls the names *Exobasidium Azaleae, E. discoideum,* and *E. Rhododendri*

[1] *loc. cit.*

appear superfluous, for their galls pass through the concavity stage and the morphological characters of the fungi concerned differ in no respect from those of *E. Vaccinii.*

Exobasidium Cassandrae was based on a leaf concavity of *Cassandra calyculata.* The new host was the sole basis for this new name and its author closed his description with the comment, "perhaps this is only a form of E. Vaccinii." Since we now regard *E. Vaccinii* as able to infect many species of the *Ericaceae,* the host alone in this case (with the morphological characters of the fungus agreeing with those of *E. Vaccinii*) does not afford sufficient justification for regarding *E. Cassandrae* as distinct from *E. Vaccinii.*

Exobasidium Arctostaphyli was founded on a leaf spot on *Arctostaphylos pungens.* As in the case of *Exobasidium Cassandrae,* there is no evidence whatever that the fungus concerned is not *E. Vaccinii,* the characters of the fungus and its work being quite those of the latter species.

The usual errors in connection with the preceding series of synonyms which are grouped together in the second division of my table are due, it seems to me, to attaching to a strange gall form—a host product—the same weight which one would give to a toadstool, and to ignoring the true fructifications of the *Exobasidium* concerned. In the taxonomy of the *Hymenomycetes,* species are based upon differences in morphological characters. It is so remarkable an innovation in our taxonomic usage in this group of plants to propose a new species which has precisely the same morphological characters as a well-known and established one that it makes it incumbent upon, and an unusual opportunity for, an author so establishing a species to show conclusively the truth of the paradox that actually good and distinct species of *Hymenomycetes* have the same morphological characters. In all the cases which have been considered, no evidence tending toward such proof has been offered. In the above, I but express the views of many of the best mycologists, who have consistently regarded the above-mentioned Exobasidium names as synonyms of *E. Vaccinii.*

Winter[1] wrote of *Exobasidium Vaccinii* in Europe where there is a similar confusion as to species, "der Pilz erzeugt ausnahmslos Formänderungen der verschiedensten Art an den von ihm bewohnten Pflanzentheilen . . . . . Ich finde zwischen den einzelnen verschiedene Nährpflanzen bewohnenden Formen keine wesentlichen Unterschiede."

The specimens which I have studied show that we have in North America perhaps three species of *Exobasidium,* two of which are rare and are present in herbaria in so few specimens that present conclusions concerning them are somewhat tentative. These species are as follows:

1. *E. Vaccinii* (Fuck.) Wor.

This species is common and wide-spread and is parasitic on many ericaceous host plants. There is as yet no evidence of which I am aware tending to show that so-called physiological races or forms with parasitism limited to a particular host exist in this species. This fungus attacks leaves developing leafy shoots, and flowers of susceptible plants, making its most successful infections when these organs are very young. The vegetative hyphae live in the infected organs between the cells, which are stimulated by the presence and activities of the parasitic hyphae to make a more or less marked hypertrophic growth response, termed a gall. The galls are of varied and sometimes strange form according to the host, the organ, and its age. The distribution of the galls upon the host is dependent upon the susceptibility of its various organs to infection.

In fruiting, the hyphae push through the epidermis to the surface and produce there a resupinate fructification which is amphigenous in the case of galls from tissues so young that they form galls of wax-like or coralloid structure, and hypophyllous on the more common leaf galls. The fructification is variable in thickness, consisting sometimes of scattered clusters of basidia but usually with hyphae present in variable quantity between the basidia so that the fructification may attain a maximum thickness of 60–70 μ, as in the case of col-

[1] In Rabenhorst, Krypt. Flora 1[1]: 322. 1884.

lections on *Vaccinium vitis-idaea.* As shown by Richards,[1] these hyphae bear simple, acicular, conidia about 6–9×1–1½ μ. Conidia are nearly always present in the preparations but have been entered only occasionally in my table. The basidia are generally 4-spored. The basidiospores from herbarium specimens are colorless, simple or with some uniseptate, 10–20×2½–5 μ, but are usually about 12–18×3–3½ μ. They are sometimes a little shorter, or a little longer, or a little thinner, or a little thicker, but are so variable within the extremes stated for different collections on the same host within the same regions or distant regions—as will be seen by reference to my table—that a moderate latitude in spore dimensions seems evident.

2. *E. Vaccinii uliginosi* Boud.

The European specimen of this species distributed from Norway in Briosi and Cavara, 'Funghi Paras.,' 261, has a resupinate, hypophyllous felty fructification, 30–45 μ thick, which is composed almost wholly of large basidia, standing close together and presenting in sections the appearance of a distinct palisade layer. This fructification begins below the epidermis and tears the cells of the latter loose and apart from each other and carries them outward between the basidia. The hymenium is abundantly fruited with basidiospores, borne two to a basidium. The spores are simple, colorless, even, curved towards the base, 18–20×6–7 μ. No conidial hyphae could be found between the basidia in this specimen.

The specimen distributed in Eriksson, 'Fungi Par. Scand.,' 286a, has similar spores 16–20×8 μ. This specimen is in poorer condition and does not show basidia clearly. In some places the fructification is composed of very fine, short-celled hyphae, which are not bearing conidia. Both the above specimens are shoot galls with leaves felty below and reddened above.

Professor Piper, 443, collected on *Vaccinium membranaceum,* at Mt. Ranier, Washington, in August, a shoot gall similar to the European specimens and having a well fruited

[1] *loc. cit.*

Exobasidium with 2-spored basidia and spores 16–20×8 μ. The fungus agrees in all respects with the specimen in Briosi and Cavara, 261. Several other collections on *Vaccinium membranaceum* of buff colored leaf concavity and leaf spot galls appear to bear *Exobasidium Vaccinii.* The very thick spores, borne two to a basidium, distinguish *E. Vaccinii uliginosi* from *E. Vaccinii.*

3. *E. Symploci* Ell. & Mart.

This fungus attacks the developing leaf buds of *Symplocos tinctoria* and deforms them into a lobed mass. In fruiting, the hyphae protrude on the surface of the mass and bear acicular, simple, colorless, slightly curved conidia, ranging from about 7×1 μ upward. The largest spores are 24×2 μ, acicular, curved, and of the same form as those of intermediate size and so on down to attached conidia. I have not found any of the largest spores attached, nor have I found basidia. In the original description the reference to spore characters is "conidia hyaline, cylindric, nearly straight, 15–21×2 μ."

I conclude that basidia have yet to be demonstrated for this fungus.

As I have had an opportunity to examine a large number of Exobasidium specimens, collected in widely separated localities, on many hosts and at various times in the growing season, it has seemed that a concise summary of the data obtained in regard to each specimen might prove useful for comparison purposes to others who study our specimens of this genus in the future. Pains have been taken to give the hosts accurately. I am indebted to Dr. J. M. Greenman for aid in host determinations in several cases.

In the matter of spores the stated dimensions are those of the preparations which were studied. No effort was made to study preparation after preparation from the same collection in order to find spores possibly larger or smaller than those of the first preparation which showed the spores well. The dimensions stated are those obtained by treating all specimens in exactly the same way and give such results as herbarium specimens afford.

TABLE I

COMPARATIVE TABLE OF DATA CONCERNING SPECIMENS OF EXOBASIDIUM EXAMINED

Host	Spore measure	Gall	Date	Locality	Coll. or herb.
EXOBASIDIUM VACCINII (FUCK.) WOR. THE FOLLOWING HAVE BEEN REFERRED HERE INVARIABLY					
Vaccinium vitis-idaea	14–16.8×2.8 μ (Wor.)	Leaf spot, leaf concavity—scurfy or felty below and reddish above—shoot gall, flower gall.	May to Sept.	Russia	Woronin's article
	12–15×3–3½ μ	Leaf spot, leaf concavity—scurfy or felty below and reddish above.	July	Germany	Krieger, Fung. Sax., 62
	12–15×3 μ	Leaf concavity, felty below, red above.	Aug.	Sweden	Romell
	12–15×3–3½ μ	Same as preceding.	Aug.	Sweden	Burt
V. vacillans	12–14×3 μ	Many leaves, felty under, reddish above.	June	Mass.	Sey. & Earle, Ec. Fung., 137a
	12×2½–3 μ	Leaf spot, scurfy below, reddish above.	July	Mass.	Sey. & Earle, Ec. Fung., 137b
	12–15×3 μ	Leaf spot, felty below, red above.	July	Mass.	Sey. & Earle, Ec. Fung., 137c
	12–15×3–3½ μ	Many leaves, felty under, reddish above.	June	Md.	Barth., Fung. Col., 3324
	15×3 μ	Same as preceding.	May	D. C.	Barth., Fung. Col., 1728
	12–18×3–4 μ	Same as preceding.	May	Md.	Barth., Fung. Col., 3231
	Conidia 6–9×1 μ	Same as preceding.	May	Mo.	Mo. B. G. Hb., 4949
V. arboreum	15×3–3½ μ	Leaf spot, scurfy below, reddish above.	April	Ala.	Ala. Biol. Surv.
	12–15×3 μ	Same as preceding.	April	Ala.	Mo. B. G. Hb., 4975
V. pennsylvanicum	12–13×3 μ	Leaf spot, scurfy below, reddish above.	.....	Wis.	Mo. B. G. Hb., 4985
	11–13×3 μ	Leaf spot, felty below, reddish above.	Aug.	Wis.	Mo. B. G. Hb., 44414
	Immature	Leaf spot, scurfy below, reddish above.	.....	N. Bruns.	Mo. B. G. Hb., 44415
	11–13×3 μ	Same as preceding.	.....	Minn.	Mo. B. G. Hb., 44416
V. stamineum	12–15×3 μ	Leaf spot, scurfy below, dark red above.	April	Ala.	Ala. Biol. Surv.
	12–15×3–4½ μ	Same as preceding.	April	Ala.	Mo. B. G. Hb., 4976
	12×3 μ	Same as preceding.	May	Ala.	Mo. B. G. Hb., 4971
	12–15×3–3½ μ	Leaf spot, scurfy below, buff and red above.	June	N. Y.	Mo. B. G. Hb., 4991

V. membranaceum	12–14×3–3½ μ	Leaf concavity, scurfy, yellowish buff.	Sept.	Wash.	Suksdorf, 448
	13–15×3 μ	Same as preceding.	Aug.	Wy.	Mo. B. G. Hb., 44413
	15–19×4–5 μ	Barely a concavity, scurfy, yellowish buff and spots red margined.	Aug.	Wash.	Suksdorf, 504
	12–18×4–5 μ	Same as noted for preceding.	Sept.	Wash.	Suksdorf, 504
	Too immature.	Leaf spot, scurfy below, yellowish.	July	Idaho	Mo. B. G. Hb., 4989
Gaylussacia frondosa	12–15×3–3½ μ	Shoot gall—all later leaves of shoot with whole of each felty below, reddish above.	June	Mass.	Bartholomew, Fung. Col., 3323
	Sterile	Leaf spot, leaf concavity, reddish above.	June	N. Y.	Mo. B. G. Hb., 4953
	12–14×3 μ	Leaf spot, leaf concavity, reddish above.	July	N. Y.	Mo. B. G. Hb., 4957
	Sterile	Leaf concavity, scurfy below, red above.	May	Fla.	Mo. B. G. Hb., 44404
	14×3 μ	Leaf spot, scurfy below, buff colored.	Sept.	Mich.	Waite, 118
	Sterile	Leaf spot, scurfy below, buff or red above.	Sept.	Mass.	Mo. B. G. Hb., 4948
G. resinosa	Immature	Whole leaves, scurfy below, reddish above.	May	Va.	Barth., Fung. Col., 3232
	Conidia 6–9×1–1½ μ	Shoot gall—whole leaves felty below, green or slightly reddened above.	May	Md.	Barth., Fung. Col., 3523
	15×3–3½ μ	Leaf concavity, felty below, red above.	May	Md.	Barth., Fung. Col., 3430
	Conidia	Leaf concavity, shoot gall of the V. vitis-idaea coralloid type.	May	Md.	Barth., Fung. Col., 3429
	Immature	Shoot gall of coralloid type, flower gall.	June	Mass.	Seymour Herb., T54
	Sterile	Leaf concavity, felty below, red above.	July	Mass.	Sey. & Earle, Ec. Fung., 488
	Conidia 6–10×1–1½ μ	Leaf concavity, shoot gall with whole leaves felty under, reddened above.	July	N. Y.	Mo. B. G. Hb., 4781
	Conidia 6–9×1 μ	Shoot gall with whole leaves felty under, reddened above.	.....	Wis.	Mo. B. G. Hb., 4961

TABLE I (Continued)

Host	Spore measure	Gall	Date	Locality	Coll. or herb.
G. resinosa —continued	10–12×2½–3 μ Conidia 6–9×1–1½μ	Shoot gall of coralloid type, leaf concavity, flower gall.	July	Maine	Seymour Herb., T55
	Conidia 6–8×1 μ	Shoot gall with whole leaves felty below.	.....	.....	Mo. B. G. Hb., 4946
Arctostaphylos uva-ursi	Sterile	Shoot gall with all leaves felty below, reddened above.	July	Wash.	Piper, 434
	12–15×3 μ	Shoot gall of the V. vitis-idaea coralloid type.	Aug.	Col.	Barth, Fung. Col., 2729
A. manganita	12×3 μ	Whole leaves felty below, reddened above.	July	Cal.	Seymour Herb.
A. nevadensis	16×4½ μ	Shoot gall of coralloid type.	July	Wash.	Suksdorf, 840
	12–14×3 μ	Shoot gall with all leaves felty below, dark red above.	Aug.	Wash.	Piper, 428
Arbutus Menziesii	12–15×2–4 μ	Leaf concavity, felty below, red above.	.....	Cal.	Ell. & Ev., N. Am. F., 1586b
Lyonia jamaicensis	15×3½ μ	Leaf concavity to leaf bags, drying reddish brown.	March	Jamaica	Mo. B. G. Hb., 44403
Rhododendron albiflorum	Spores soon 3-septate 15–22×4–6 μ Basidia 4-spored	Leaf spots, scurfy below, buff colored.	Sept.	Wash.	Suksdorf, 841
	12–20×4–5 μ and as above	Leaf spots, scurfy below, buff colored.	Sept.	Wash.	Suksdorf, 449
R. canadense	Conidia	Leaf spot, scurfy below, reddish above.	Sept.	Newf.	Mo. B. G. Hb., 42608
		Same as preceding.	Aug.	Newf.	Mo. B. G. Hb., 4981
R. maximum	12–15×4 μ	Leaf concavity, red.	July	N. Car.	Mo. B. G. Hb., 4951

EXOBASIDIUM VACCINII (FUCK.) WOR. THE FOLLOWING SYNONYMS ARE BASED ON GALL FORMS AS STATED:					
Exobasidium Azaleae Peck, = E. discoideum Ell.					
Azalea nudiflora	15–16×3 μ	Terminal bags, lateral leaf bags.	May	Ala.	Ala. Biol. Surv.
	13–18×3–4½ μ	Leaf bag, scurfy leaf spots, reddish above.	May	Ala.	Mo. B. G. Hb., 4964
	Sterile	Leaf bag suspended by a point.	April	Ala.	Mo. B. G. Hb., 4963
	Sterile	Flowers modified into obconic galls.	June	Mass.	A. B. Seymour Herb.
A. cult. sp.	12–15×3–3½ μ	Flower and leaf bag galls.	June	Mass.	Sey. & Earle, Ec. Fung., 489
A. viscosa	13–18×3–3½ μ	Bag gall, suspended from leaf.	July	N. J.	E. & Ev., N. Am. F., 1718
	Sterile	Bag gall, suspended from leaf.	May	Miss.	Mo. B. G. Hb., 4970
	Conidia	Flower and leaf bag galls.	April	Miss.	Mo. B. G. Hb., 4960
	Sterile	Bag gall, suspended from leaf.	Aug.	Mass.	Mo. B. G. Hb., 44405
	18×3½ μ	Leaf spots, scurfy below, reddened above.	Sept.	Mass.	Mo. B. G. Hb., 44410
Exobasidium Rhododendri Cramer					
Rhododendron ferrugineum	12–15×3–3½ μ	Leaf concavity, bag gall suspended from leaf.	Sept.	Switz.	Rabenhorst, Fung. Eur., 1910
	13–15×3–4 μ	Bag gall, suspended from leaf.	Sept.	Germ.	Magnus, Mo. B. G. Hb.
	14×3 μ	Bag gall, suspended from leaf.	Aug.	Austria	Magnus, Mo. B. G. Hb.
	Sterile	Bag gall, suspended from leaf.	Aug.	Switz.	Kunze, Fung. Sel. Ex. 302
Exobasidium Peckii Halst.					
Andromeda Mariana	12–13×3 μ	Leaf concavity, reddened above; flower gall—flower organs all enlarged.	May	Fla.	A. B. Seymour Herb.
	11–15×3 μ	Same gall forms as the preceding.	May	Fla.	Mo. B. G. Hb., 4966
	12–18×3–4 μ	Same gall forms as the preceding.	June	N. Y.	Sey. & Earle, Ec. Fung., 487
	12–18×3–3½ μ	Leaf concavity, felty below, reddened above.	June	N. J.	Ell. & Ev., Fung. Col., 1210
	Conidia 6–9×1–1½ μ	Leaf concavity, reddened above.	June	Fla.	Mo. B. G. Hb., 4954
Lyonia ferruginea	16–18×4 μ	Flower gall, 2½×2½ cm.—all the organs present and proportionately enlarged.	May	Ga.	U. S. Dept. of Agr.

TABLE I (Continued)

Host	Spore measure	Gall	Date	Locality	Coll. or herb.
Lyonia ferruginea —continued	15×3½–4 μ	Same as above—3–5 cm. long, 1–2½ cm. thick.	June	Ga.	Mo. B. G. Hb., 4955
	12×3½ μ	Flower gall of same type as preceding.	April	Fla.	Mo. B. G. Hb., 4962
		Flower gall of same type as preceding.	.....	Fla.	Mo. B. G. Hb., 44409
Exobasidium Andromedae Peck					
Andromeda ligustrina	15–18×3–3½ μ	Bag gall, terminal on shoot.	June	Mass.	H. L. Jones
	15–18×3–3½ μ	Bag gall, terminal on shoot.	June	Mass.	Rush.
	Conidia	Bag gall, terminal on shoot.	June	Mass.	Duggar, Mo. B. G. Hb.
	17×3½ μ	Leaf bag, terminal bag.	June	N. Y.	Shear, N. Y. Fung., 117
	12–16×3 μ	Bag gall, terminal on shoot.	.....	N. J.	Ellis, N. Am. Fung., 107
	12–15×3½–4 μ	Bag gall in the place of a leaf.	April	Fla.	Mo. B. G. Hb., 44326
Menziesia glabella	10–13×2–2½ μ 10–18×1½–2½ μ	Bag gall, terminal on shoot. Leaf concavity of E. Vaccinii type.	Aug.	Idaho	Piper, 772
Exobasidium Cassandrae Peck					
Cassandra calyculata	12–15×3–4 μ	Leaf concavity, felty below, red above.	.....	N. Y.	Peck, Ellis N. Am. F. 722
	12–15×3–4½ μ	Leaf concavity, scurfy below, red above.	.....	N. Y.	Clinton
	15×3½ μ	Leaf concavity, felty below, red above.	Aug.	Canada	Ell. & Ev. N. Am. F., 2312a
	15×3–4½ μ	Leaf concavity, felty below, red above.	July	Mich.	Trelease, Mo. B. G. Hb.
	12×3 μ	Whole leaf, felty below, red above.			
	Conidia	Shoot gall—all leaves felty under, reddish above.	.....	Newf.	Robinson & von Schrenk, Mo. B. G. Hb.
	14×3½ μ	Leaf spot, felty below, red above.	July	Russia	Fung. Rossiae Ex. 72
Exobasidium Arctostaphyli Harkn.					
Arctostaphylos pungens	12–17×3–5 μ	Leaf spot, scurfy below, red above.	.....	Cal.	Ell. & Ev., N. Am. F. 1586a
	12–18×4½ μ	Leaf spot, scurfy below, red above.	.....	Cal.	Harkness, Mo. B. G. Hb.

Exobasidium Cassiopes Peck					
Cassiope Mertensiana	12–13×3 μ	Shoot gall of the V. vitis-idaea coralloid type.	Aug.	Wash.	Suksdorf, 501
	12–13×3 μ	Shoot gall like the preceding.	Aug.	Wash.	Piper, 771
Exobasidium Oxycocci Rostrup					
Vaccinium macrocarpon	15×3–3½ μ Conidia 6–9×1–1½ μ	Shoot gall of the V. vitis-idaea coralloid type.	.....	Mass.	Minns in U. S. Dept. of Agr. Hb.
	12–15×3 μ	Shoot gall like the preceding.	Sept.	Mass.	Trelease, Mo. B. G. Hb.
	12×3 μ	Leaf spot, leaf concavity, scurfy, red above.	Aug.	Mass.	Ell. & Ev., N. Am. F. 2312b
V. intermedium	12–14×3 μ	Shoot gall of coralloid type.	June	Wash.	Piper, 39
Exobasidium Karstenii Sacc. & Trott. = E. Andromedae Karst. non Peck					
Andromeda polifolia	12×3 μ	Shoot gall, coralloid—all the leaves reddish livid.	July	Finland	Karsten
	12–15×3 μ	Shoot gall like the preceding	July	Finland	Thuem., Myc. Univ. 1110
	Sterile	Shoot gall like the preceding.	June	N. H.	Mo. B. G. Hb., 4778
Exobasidium Vaccinii myrtilli (Fuck.) Juel					
Vaccinium Myrtillus	13–15×3 μ	Shoot gall with all leaves felty below, reddened above.	June	Germany	Krieger, Fung. Sax. 665
	Conidia 6–9×1–1½ μ	Shoot gall like the preceding.	May	Germany	Thuem., Myc. Univ. 115
V. uliginosum	12–15×3–4½ μ	Leaf concavity; shoot gall like above.	July	Germany	Krieger, Fung. Sax., 768
	12–14×3 μ	Shoot gall with all leaves felty below, reddish above.	.....	Finland	Karsten
	10–12×3 μ	Shoot gall like the preceding.	.....	Sweden	Eriksson, Fung. Par., 286b
V. deliciosum	11–12×3 μ Conidia 6–8×1 μ	Shoot gall like the preceding.	Aug.	Wash.	Piper, 842
V. sp.	12–14×3–3½ μ	Shoot gall redder above than preceding.	Sept.	Wash.	Suksdorf, 447

TABLE I (Continued)

Host	Spore measure	Gall	Date	Locality	Coll. or Herb.
		EXOBASIDIUM VACCINII ULIGINOSI BOUD.			
Vaccinium uliginosum	18–20×6–7 μ Basidia 2-spored	Shoot gall with all leaves felty below, red above.	Aug.	Norway	Briosi & Cavara, Fung. Par., 261
V. Myrtillus	15–17×7–8 μ	Shoot gall like the preceding.	.....	Norway	Eriksson, Fung. Par., 286a
V. membranaceum	16–20×8 μ Basidia 2-spored	Shoot gall like the preceding.	Aug.	Wash.	Piper, 443
		EXOBASIDIUM SYMPLOCI ELLIS & MART.			
Symplocos tinctoria	7–14×1½–2 μ, perhaps all are conidia	Leaf bud gall, mass 3×2 cm.	March	Fla.	Ell. & Ev., N. Am. F., 1696
	As above	Same as preceding.	March	Fla.	Mo. B. G. Hb., 4968
	8–24×1½–2 μ, perhaps all are conidia	Same as preceding.	April	Ala.	Mo. B. G. Hb., 4969
	Immature	Same as preceding.	April	Ind.	Rhodes, Mo. B. G. Hb.

Systematic Summary

1. Exobasidium Vaccinii Fuck. ex. Wor. Naturforsch. Ges. Freiburg Verhandl. **4**: 397–416. *pl. 1–3.* 1867. Plate 21.

Fusidium Vaccinii Fuck. Bot. Zeit. **19**: 251. 1861.—*Exobasidium Andromedae* Peck, Buffalo Soc. Nat. Hist. Bul. **1**: 63. 1873; N. Y. State Mus. Rept. **26**: 73. 1874.—*E. Azaleae* Peck, Buffalo Soc. Nat. Hist. Bul. **1**: 63. 1873; N. Y. State Mus. Bul. **26**: 72. 1874.—*E. discoideum* Ellis, Torr. Bot. Club Bul. **5**: 46. 1874.—*E. Rhododendri* Cramer in Rabenh. Fung. Eur. 1910. 1875.—*E. Andromedae* Karst. in De Thuemen, Myc. Univ. 1110. 1878; Finland Natur och Folk Bidrag **37**: 153. 1882.—*E. Karstenii* Sacc. & Trott. in Sacc. Syll. Fung. **21**: 420. 1912.—*E. Cassandrae* Peck, N. Y. State Mus. Bul. **29**: 46. 1874.—*E. Arctostaphyli* Harkn. Calif. Acad. Sci. Bul. **1**: 30. 1884.—*E. Myrtilli* (Thuem.) Karst. Finlands Natur och Folk Bidrag **37**: 152. 1882.—*E. Vaccinii Myrtilli* (Fuck.) Juel, Svensk. Bot. Tids. **6**: 364. 1912.—*E. Oxycocci* Rostr. Bot. Tidsskr. **14**: 243. 1885.—*E. Cassiopes* Peck, N. Y. State Mus. Rept. **45**: 24. 1893.—*E. Peckii* Halst. Torr. Bot. Club Bul. **20**: 437. 1893.

Illustrations: Woronin. *loc. cit.*—Richards, Bot. Gaz. **21**: *pl. 6. f. 1–20.*—Petri, Ann. Myc. **5**: 342–346.—Brefeld, Untersuch. Myk. **8**: *pl. 1. f. 17–22.*—Duggar, Fung. Dis. *f. 215, 216.*—Shear, U. S. Dept. Agr., Bur. Pl. Ind. Bul. 110: *pl. 7. f. A–D.*—Juel, Svensk. Bot. Tids. **6**: 353–372. *f. A–C.*—Engl. & Prantl, Nat. Pflanzenfam. (**I.** 1**): 104. *f. 65.*—Other illustrations in many text-books. References to other illustrations in Sacc. Syll. Fung. **19**: 694.

Fructifications hypophyllous or amphigenous, resupinate, effused, scurfy or felty and compact, grayish, consisting of somewhat scattered clusters of basidia or of basidia and fine, suberect, more or less interwoven and branched hyphae which bear conidia and give to the fructification a maximum thickness ranging up to 60–70 μ; basidia with 4 sterigmata usually; basidiospores colorless, simple or with some 1-septate, 10–20$\times$2½–5 μ, but usually about 12–18$\times$3–3½ μ, becoming 3-septate in germinating; conidia simple, 6–9$\times$1–1½ μ.

Parasitic in leaves, young shoots, and flowers of various ericaceous hosts, and stimulating the infected parts to the production of leaf, shoot, or flower galls which bear the fructifications on their surface. Leaf galls are usually somewhat reddish on the upper side and bear the fructification on the lower side.

From Newfoundland to Florida and westward to California and Washington, also in Jamaica.

I have referred here, with some doubt, the *Exobasidium* causing yellow-buff leaf spot galls on *Rhododendron albiflorum,* collected on mountains in Washington by W. N. Suksdorf. The basidia are 20–30×6 μ, with 4 prominent sterigmata; the basidiospores are mostly 18–21×4½–6 μ, and are nearly all 3-septate. Some of these spores are germinating, hence the septation of the spores may possibly be due to their over maturity when collected, combined with weather conditions at that time favorable to germination. Other collections which show the full series of gall forms on this host are desirable and should give the needed information in regard to septation of the spores.

Specimens examined:

Exsiccati: Ellis, N. Am. Fung., 107, 722; Ell. & Ev., N. Am. Fung., 1586a, 1586b, 1718, 2312a, 2312b; Ell. & Ev., Fung. Col., 220, 1210; Bartholomew, Fung. Col., 1728, 2729, 3231, 3232, 3323, 3324, 3429, 3430, 3523; Seymour & Earle, Econ. Fung., 137a, 137b, 137c, 487, 488, 489; Shear, N. Y. Fung., 117; De Thuemen, Myc. Univ., 115, 210, 1110, 1808; Eriksson, Fung. Par., 286b; Jaczewski, Komarov & Tranzschel, Fung. Rossiae Ex., 72; Kunze, Fung. Sel. Ex., 302; Krieger, Fung. Sax., 62, 665, 768; Rabenhorst, Fung. Eur., 1910; Romell, Fung. Scand., 38.

Austria: On *Rhododendron ferrugineum,* Tyrol, *P. Magnus* (in Mo. Bot. Gard. Herb., 4988).

Germany: On *Vaccinium vitis-idaea,* Königstein, *Krieger,* Krieger, Fung. Sax., 62; Bavaria, *De Thuemen,* Myc. Univ., 910; on *Rhododendron ferrugineum, P. Magnus;* on *Vaccinium Myrtillus,* Leipzig, *G. Winter,* De Thuemen, Myc.

Univ., 115; Königstein, *Krieger,* Fung. Sax., 665; on *V. uliginosum,* Altenberg, *Krieger,* Fung. Sax., 768.

Russia: On *Cassandra calyculata,* Novgorod, Jaczewski, Fung. Rossiae Ex., 72.

Finland: On *Vaccinium uliginosum,* Mustiala, *P. A. Karsten;* on *Andromeda polifolia,* Mustiala, *P. A. Karsten;* and also in De Thuemen, Myc. Univ., 1110.

Sweden: On *Vaccinium vitis-idaea,* Femsjö, *L. Romell;* Upsala, *E. A. Burt;* on *Andromeda polifolia, L. Romell,* Romell, Fung. Scand., 38; on *Vaccinium uliginosum,* Eriksson, Fung. Par. Scand, 286b.

Switzerland: On *Rhododendron ferrugineum,* Luzern, *G. Winter* in Kunze, Fung. Sel. Ex., 302; same host, Maderaner Thal, *Cramer,* Rabenhorst, Fung. Eur., 1910.

Canada: on *Cassandra calyculata,* London, *J. Dearness,* Ell. & Ev., N. Am. Fung., 2312a.

Newfoundland: on *Cassandra calyculata,* Pennie's River, *B. L. Robinson & H. von Schrenk* (in Mo. Bot. Gard. Herb., 4779); on *Rhododendron canadense,* Bluff Head, *A. C. Waghorne, 940* (in Mo. Bot. Gard. Herb., 42608); Virginia Water, *B. L. Robinson & H. von Schrenk* (in Mo. Bot. Gard. Herb., 4981).

New Brunswick: on *Vaccinium pennsylvanicum, Hays, 16* (in Mo. Bot. Gard. Herb., 44415).

Maine: on *Gaylussacia baccata,* Biddeford, *Mrs. A. M. Pier* (in Seymour Herb., T55).

New Hampshire: on *Andromeda polifolia,* Shelburne, *H. von Schrenk* (in Mo. Bot. Gard. Herb., 4778).

Massachusetts: on *Vaccinium vacillans,* Arlington, Magnolia, and Medford, *A. B. Seymour,* Sey. & Earle, Econ. Fung., 137a, 137b, 137c respectively; Plymouth, *E. Bartholomew,* Fung. Col., 3324; Weston, *A. B. Seymour, T56* (in Seymour Herb.); Rafes Chasm, *A. B. Seymour, T58* (in Seymour Herb.); Middlesex Falls, *J. G. Jack* (in Seymour Herb.); on *V. macrocarpon,* Woods Hole, *W. Trelease* (in Mo. Bot. Gard. Herb., 4982); Chatham, *Miss Minns,* and also (in U. S. Dept. Agr. Herb.); Harwich, *B.D.Halsted,* Ell.& Ev.,N.Am. Fung., 2312b; Waverly, *A. B. Seymour, T60* (in Seymour

Herb.); on *V. pennsylvanicum,* Rafes Chasm, *A. B. Seymour T59* (in Seymour Herb.); on *Gaylussacia frondosa,* Woods Hole, *W. Trelease* (in Mo. Bot. Gard. Herb., 4948); Plymouth, *E. Bartholomew,* Fung. Col., 3323; on *G. resinosa,* Manchester, *W. C. Sturgis,* Sey. & Earle, Econ. Fung., 488; Falmouth, *A. B. Seymour, T53* (in Seymour Herb.); Woods Hole, *A. B. Seymour, T54* (in Seymour Herb.); Dartmouth, *W. G. Farlow* (in Seymour Herb.); Brewster, *W. G. Farlow* (in Seymour Herb.); on *Andromeda ligustrina,* Cambridge, *Mr. Rush;* Dedham, *H. L. Jones,* and also *B. M. Duggar* (in Mo. Bot. Gard. Herb., 44411); Woods Hole, *W. Trelease* (in Mo. Bot. Gard. Herb., 44410); Hampden, *A. B. Seymour, T51* (in Seymour Herb.); Granville, *A. B. Seymour* (in Seymour Herb.); on *Rhododendron cult. sp.,* Brookline, *A. B. Seymour,* Sey. & Earle, Econ. Fung., 489; on *R. nudiflorum,* Granville, *A. B. Seymour* (in Seymour Herb.); on *R. viscosum,* Woods Hole, *W. Trelease* (in Mo. Bot. Gard. Herb., 44405, 44408).

New York: on *Vaccinium stamineum,* Ithaca, *W. Trelease* (in Mo. Bot. Gard. Herb., 4991); on *Gaylussacia frondosa,* Eastport, *J. Schrenk* (in Mo. Bot. Gard. Herb., 4953); Eastport, *H. von Schrenk* (in Mo. Bot. Gard. Herb. 4957); on *G. resinosa,* Deer Park, *H. von Schrenk* (in Mo. Bot. Gard. Herb., 4781); on *Andromeda ligustrina,* Alcove, *C. L. Shear,* N. Y. Fung., 117; on *A. Mariana,* Westbury, *F. C. Stewart,* Sey. & Earle, Econ. Fung., 487; on *Cassandra calyculata,* Adirondack Mts., *C. H. Peck,* Ellis, N. Am. Fung., 722; Buffalo, *G. W. Clinton.*

New Jersey: on *Andromeda ligustrina, Ellis,* N. Am. Fung., 107; on *A. Mariana,* Newfield, *Ellis,* Ell. & Ev., Fung. Col., 1210; on *Rhododendron viscosum,* Newfield, *Ellis,* Ell. & Ev., N. Am. Fung., 1718; and (in Mo. Bot. Gard. Herb., 4959).

Maryland: on *Vaccinium vacillans,* Rosecraft, *Bartholomew,* Fung. Col., 3231; on *Gaylussacia resinosa,* Lanham, *E. Bartholomew,* Fung. Col., 3429, 3430; *Bartholomew & Swingle,* Fung. Col., 3523.

District of Columbia: on *Vaccinium vacillans,* Takoma Park, *C. L. Shear,* Fung. Col., 1728.

Virginia: on *Gaylussacia resinosa,* Vienna, *E. Bartholomew,* Fung. Col., 3232.

North Carolina: on *Rhododendron maximum, H. von Schrenk* (in Mo. Bot. Gard. Herb., 4951); on *R. nudiflorum, H. von Schrenk* (in Mo. Bot. Gard. Herb., 4950).

Georgia: on *Lyonia ferruginea,* Brunswick, comm. by U. S. Dept. Agr. Herb.; *W. Trelease* (in Mo. Bot. Gard. Herb., 4955).

Florida: on *Gaylussacia frondosa,* Dunedin, *S. M. Tracy, 6649* (in Mo. Bot. Gard. Herb., 44404); on *Andromeda ligustrina,* St. Leo, *Rev. Jerome* (in Mo. Bot. Gard. Herb., 44326); on *A. Mariana,* White Springs, *H. H. Hume, 88* (in Mo. Bot. Gard. Herb., 4966), and also (in Seymour Herb.); *Chapman* (in Mo. Bot. Gard. Herb., 4954); on *Lyonia ferruginea, Chapman* (in Mo. Bot. Gard. Herb., 44409).

Alabama: on *Vaccinium arboreum,* Auburn, *Ala. Biol. Surv.,* and also (in Mo. Bot. Gard Herb., 4975); on *V. stamineum,* Auburn, *Ala. Biol. Surv.,* and also (in Mo. Bot. Gard. Herb., 4976); Auburn, *F. S. Earle & L. M. Underwood* (in Mo. Bot. Gard. Herb., 4971); on *Rhododendron nudiflorum,* Auburn, *Ala. Biol. Surv.,* and also (in Mo. Bot. Gard. Herb., 4964, 4963).

Mississippi: on *Rhododendron viscosum,* Ocean Springs, *F. S. Earle* (in Mo. Bot. Gard. Herb., 4970); and *S. M. Tracy* (in Mo. Bot. Gard. Herb., 4960).

Michigan: on *Galylussacia frondosa,* Lansing, *M. B. Waite, 118* (in U. S. Dept. Agr. Herb.); on *G. resinosa,* Agricultural College, *G. H. Hicks* (in Seymour Herb.); on *Cassandra calyculata,* Republic, *W. Trelease* (in Mo. Bot. Gard. Herb., 4983); Agricultural College, *G. H. Hicks* (in Seymour Herb.).

Minnesota: on *Vaccinium pennsylvanicum,* Hokal, *L. H. Pammel* (in Mo. Bot. Gard. Herb., 44416).

Wisconsin: on *V. pennsylvanicum,* La Crosse, *L. H. Pammel* (in Mo. Bot. Gard. Herb., 44414); Kirtland, (in Mo. Bot.

Gard. Herb., 4985); on *Gaylussacia resinosa,* Kirkland (in Mo. Bot. Gard. Herb., 4961).

Missouri: on *Vaccinium vacillans,* Crystal City, (in Mo. Bot. Gard. Herb., 4949).

Wyoming: on *V. membranaceum,* Teton Mts., *A. Nelson, E. Nelson, 6525* (in Mo. Bot. Gard. Herb., 44413).

Idaho: on *V. membranaceum,* Forest, Nez Perces Co., *A. A. & E. G. Heller, 3465* (in Mo. Bot. Gard. Herb., 4989); on *Menziesia glabella,* Bitter Root Mt., *C. V. Piper, 772.*

Colorado: on *Arctostaphylous uva ursi,* Glacier Lake, *Bartholomew & Bethel,* Fung. Col., 2729.

Washington: on *Vaccinium deliciosum,* Mt. Rainier, *C. V. Piper, 842;* on *V. membranaceum,* Mt. Paddo, *W. N. Suksdorf, 448;* Chiquash Mts., *W. N. Suksdorf, 504;* on *Vaccinium sp.,* probably *V. membranaceum,* Mt. Paddo, *W. N. Suksdorf, 447;* on *V. intermedium,* Seattle, *C. V. Piper, 39;* on *Arctostaphylos uva ursi,* Orchard Point, *C. V. Piper, 434;* on *A. nevadensis,* Mt. Paddo, *W. N. Suksdorf, 840;* Longwire Springs, *C. V. Piper, 428;* on *Cassiope Mertensiana,* Chiquash Mts., Skamania Co., *W. N. Suksdorf, 501;* Olympic Mts., *C. V. Piper, 771;* on *Rhododendron albiflorum,* Chiquash Mts., Skamania Co., *W. N. Suksdorf, 841;* Mt. Paddo, *W. N. Suksdorf, 449.*

California: on *Arctostaphylos pungens, H. W. Harkness* (in Mo. Bot. Gard. Herb., 4972); and also Ell. & Ev., N. Am. Fung., 1586a; on *A. manganita,* Sisson's, Siskiyou Co., *W. C. Blasdale* (in Seymour Herb.); on *Arbutus Menziesii, H. W. Harkness,* Ell. & Ev., N. Am. Fung., 1586b.

Jamaica: on *Lyonia jamaicensis,* Cinchona, *H. von Schrenk* (in Mo. Bot. Gard. Herb., 44403).

2. **E. Vaccinii uliginosi** Boud. Soc. Bot. Fr. Bul. 41: CCXLIV. 1894.

Illustrations: Juel, Svensk. Bot. Tids. **6**: 353–372. *pl. 7. f. 5. text. f. D.*

Fructification hypophyllous, resupinate on the whole lower surface of the leaves, felty, 30–45 μ thick, composed of large basidia arranged side by side in a compact hymenium; basidia

with 2 sterigmata; spores colorless, even, curved towards the base, 16–20 × 7–8 μ.

Parasitic on *Vaccinium membranaceum,* which produces shoot galls with all the later leaves of the gall red on the upper side, felty below, and but slightly, if at all, deformed.

Mt. Rainier, Washington. August.

In the original description of this species, the spore dimensions are stated as 25–32 × 8–12 μ. The European specimens in the exsiccati cited below, which European authors refer here, have spores of the dimensions of the American collection. Shoot galls of the type stated are the only form known to be caused by this species, but other forms may yet be found.

Specimens examined:

Exsiccati: Briosi & Cavara, Fung. Par., 261; Eriksson, Fung. Par. Scand., 286a under the name *Exobasidium Vaccinii.*

Norway: on *Vaccinium Myrtillus,* Eriksson, Fung. Par. Scand., 286a; on *V. uliginosum, G. von. Lagerheim,* Briosi & Cavara, Fung. Par., 261.

Washington: on *Vaccinium membranaceum,* Mt. Rainier, *C. V. Piper, 443.*

3. **E. Symploci** Ell. & Mart. Am. Nat. **18:** 1147. 1884.

Fructification amphigenous, resupinate, effused, consisting of lax, slender, colorless hyphae which bear solitary conidia at the tips of very short, lateral, ascending branches; conidia colorless, even slightly curved, acicular, 7–24×1–2 μ; basidia and basidiospores unknown.

Parasitic on *Symplocos tinctoria* which produces bud galls 3–3½ cm. in diameter, lemon yellow, subglobose and sublobate.

Florida, Alabama, and Indiana. March and April.

In the original description it is stated that the galls are distorted flower buds. In a specimen collected in Indiana, the gall is a partially developed leaf bud.

Specimens examined:

Exsiccati: Ell. & Ev., N. Am. Fung., 1696.

Florida: on *Symplocos tinctoria,* Green Cove Springs, *G. Martin* (in Mo. Bot. Gard. Herb., 4968); and in Ell. & Ev., N. Am. Fung., 1696.

Alabama: on *Symplocos tinctoria,* Auburn, *Ala. Biol. Surv.* (in. Mo. Bot. Gard. Herb., 4969).

Indiana: on *Symplocos tinctoria,* Robertsdale, *A. M. Rhodes* (in Mo. Bot. Gard. Herb., 741178).

SPECIES IMPERFECTLY KNOWN

E. decolorans Harkness, Cal. Acad. Sci. Bul. 1: 31. 1884.

"Receptaculum effused, producing conspicuous yellowish-white, orbicular spots, 1–2 cm. in diameter, not at all distorting the leaf; spores appearing upon the under surface, hyaline, straight, μ 7–8 $\times$ 4–5.

"On living leaves of Rhododendron occidentale. Tamalpais [Cal.]. Autumn. 2887."

The above is the original description. I have seen no specimens referable here nor on the host stated.

EXCLUDED SPECIES

E. mycetophilum Peck ex Burt, Torr. Bot. Club Bul. 28: 285–287. *pl. 23.* 1901.

Tremella mycetophila Peck, N. Y. State Mus., Bul. 28: 53. *pl. 1. f. 4.* 1879.

This curious structure on *Collybia dryophila,* I no longer regard as parasitic but, rather, as a teratological production of *C. dryophila,* induced by protracted wet weather during development of the fructification.

(To be continued.)

Explanation of Plate

PLATE 21.

This plate is a photographic reproduction, ×⅘, of Plate 1 by Woronin[1] of the various galls produced by *Vaccinium vitis-idaea* when parasitized by *Exobasidium Vaccinii*. The original plate is colored and with all figures natural size; red colors of the original have photographed light colored.

Fig. 1. Leaf spot gall, on left side of uppermost leaf; the leaf is reddish on the upper side in the infested area, not deformed, and was felty or scurfy on the lower side.

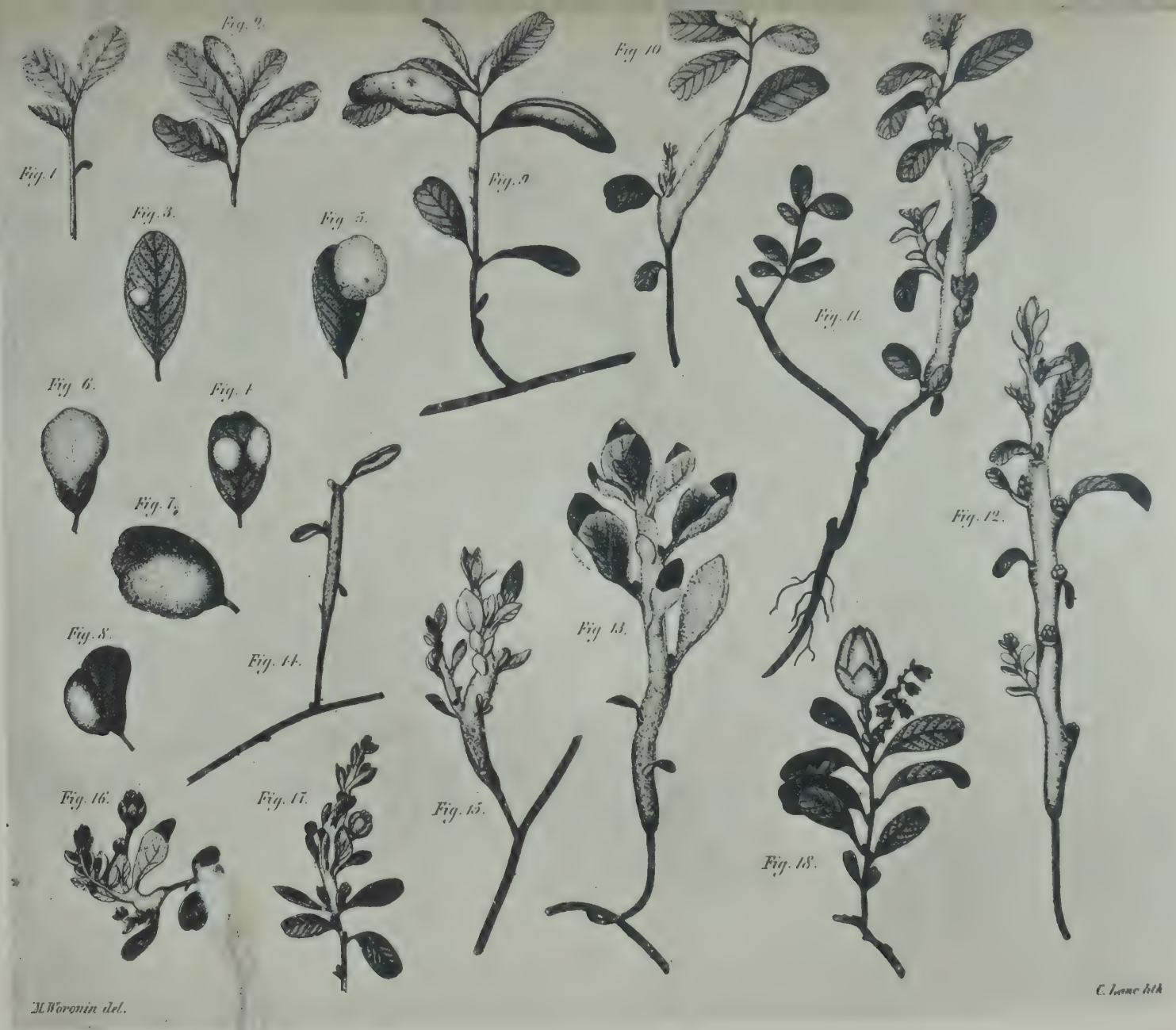
Figs. 2–9. Leaf concavity galls. More or less deformation of the infected region is present here.

Figs. 10–15. Shoot galls of the wax-like or coralloid type. Extended portions of leafy shoots are infected. Figure 11 shows whole branchlets completely hypertrophied.

Figs. 16–17. Flower galls borne on, and a part of, shoot galls.

Fig. 18. Flower gall. Local infection of a single flower, noted as the only such instance observed.

[1] *loc. cit.*



BURT—THELEPHORACEAE OF NORTH AMERICA